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BUTTERFLY MIGRATIONS IN BRITISH GUIANA

By T. A. W. Davis
(*South Mullock, Haverfordwest, Pembrokeshire*)

[Communicated by Dr. C. B. Williams, F.R.S.]

Introduction

From 1925 to 1939 I served as a forest officer in British Guiana, and from December, 1931 to January, 1939 my headquarters were at His Majesty's Penal Settlement, Mazaruni, in the Bartica district. The Settlement is a forest clearing about 140 acres in extent on the north bank of the Mazaruni River near its confluence with the Essequibo, about 40 miles from the sea coast. At headquarters I had frequent opportunities for observing butterfly migration, but on forest expeditions conditions were unfavourable except on days spent in travelling by river. All my observations were made in the lowland tropical forest region, and I saw flights of *Phoebis* spp. only. The sketch map (fig. 1) shows the localities and figure 2 the seasons and directions. In describing flights I have used the words " thin ", " definite ", *etc.* in the sense defined by Williams (1958 : 103–4).

Climate

Throughout the coastal and lowland forest regions of British Guiana there are two rainy and two dry seasons. The rainy months are December, January, May, June and July. In December the rainfall is sometimes only moderate and January may be dry, but the long rains have not been known to fail. At the Settlement, a first-class meteorological station, the average annual rainfall, 1919–38, was 100·3 inches : its seasonal distribution is shown in Table I. There is much variation in the monthly averages from year to year ; June is the most consistent month and is always wet.

Table I.—*Seasonal distribution of rainfall at H.M.P.S., Mazaruni*, 1919–38

Season :	Rainfall (inches)	Monthly average
Short rains (Dec.–Jan.) .	20·1	10·05
Short dry (Feb.–April) .	17·7	5·90
Long rains (May–July) .	36·1	12·03
Long dry (Aug.–Nov.) .	26·4	6·60
Year . .	100·3	8·36

The prevailing wind is the NE. trade, which is strong only during squalls, which occur frequently with thunderstorms in the afternoon during the long dry season and occasionally at any time. It is often calm during the long rains and at the beginning of the long dry season.

Identification

I did not collect any migrant butterflies and my conclusions regarding their identities are based on specimens in the British Museum (Natural History), especially those collected by the Oxford University Expedition to British Guiana, of which I was a member, in Moraballi River and adjacent reaches of the Essequibo in 1929. On the assumption that the white distal half of the fore wing was a reliable character for distinguishing *Phoebis statira* (Cramer) from *P. eubule* (L.) in the field, I believed at the time my observations were made that the latter species was far more abundant and often the only sulphur butterfly in a flight. But in most male specimens of *P. statira* from British Guiana the distal half of the fore wing is not white, only a little paler than the rest of the wing, so that in the field it would be impossible to distinguish them in flight from *P. eubule.* The number of specimens in the British Museum suggest that *P. statira* is much the commoner species : both sexes are well represented, including some taken by the Oxford University Expedition, whereas there are only three *P. eubule,* all males, from the Demerara River. Both sexes of a third sulphur yellow species, *P. trite* (L.), are represented, including one male taken by the Oxford University Expedition. The orange-yellow *P. agarithe* (Boisduval) was also taken by the expedition, but not *P. philea* (L.), another orange-yellow species which has been captured from migrating flights (Cleare, 1929).

Records in the literature of *P. eubule* flights do not state that specimens were captured and authoritatively identified. Williams (1917) recorded a flight he saw at Issororo, North-Western District, in early August, 1916 as *P. eubule* owing to a wrong local determination of the specimens he obtained, but when he re-examined them in England later they proved to be *P. statira* (Williams, 1923). The same error in identification may have occurred in the case of two flights of *P. eubule,* described from reports in a local scientific journal (Williams, 1917), and one that occurred in June, 1915 (Cleare, 1929). Cleare has recorded three flights from which *P. statira* were captured, including a remarkable one of several species but principally of *P. statira* : besides butterflies of other genera and the moth *Urania leilus* (L.), he took 53 *P. statira,* 4 *P. eubule,* 2 *P. philea,* and 1 *P. agarithe.* This is the only fully authenticated record I can find of *P. eubule* being captured from a migratory flight in British Guiana. Orange-yellows accompany most flights of sulphurs in small numbers, the proportion being one in a hundred or fewer. Another *P. philea* was taken at Kartabo with four *P. statira* on 15th August, 1926 (Cleare, 1929). It is therefore probable that most flights of sulphurs consist principally of *P. statira* and orange-yellows with them may be *P. philea, P. agarithe,* or both.

MIGRATION IN THE BARTICA DISTRICT

1932.—Migration was first noted on 7th August, when a definite flight was seen crossing the river from north to south between the Settlement and Kamaria on the Cuyuni River nine miles to the west. Butterflies passed continually, singly and in twos and threes. A similar movement occurred at the Settlement, on the following day, of sulphurs with an occasional orange-yellow. The southward migration continued throughout August, definite some days, thin on others. In September it became extremely thin : I often crossed the Mazaruni River from the Settlement, and usually saw one or two sulphurs, flying south, during a crossing until the 14th.

1933.—I saw no flights up to the second week in June, and was absent from the colony thereafter until late January, 1934.

1934.—I was absent from the Settlement for six weeks in March and April, and I saw no migration later in the year. August and September were unusually wet.

1935.—Migration was first seen on 30th June, when it was definite ; it was still in progress when I left the Settlement for the Demerara River on 29th August, sometimes thin or very thin but often definite, between south-east and south. On 10th July I set out at noon from the Arakwa River, a small tributary of the Essequibo, to return by river to the Settlement about 15 miles south. A definite flight of sulphurs was crossing the Essequibo obliquely from the west bank all the way, heading SSE.

1936.—The only year in which, in the Bartica district, I observed migration during the short dry season. On 20th January I noted a very thin NNW. flight of sulphurs, and on the 30th at Turtruba Rapids, Mazaruni River, five miles south-west of the Settlement, there was a definite NNW. movement which backed to WNW. when I was returning in the afternoon, more than 12 butterflies being often in sight

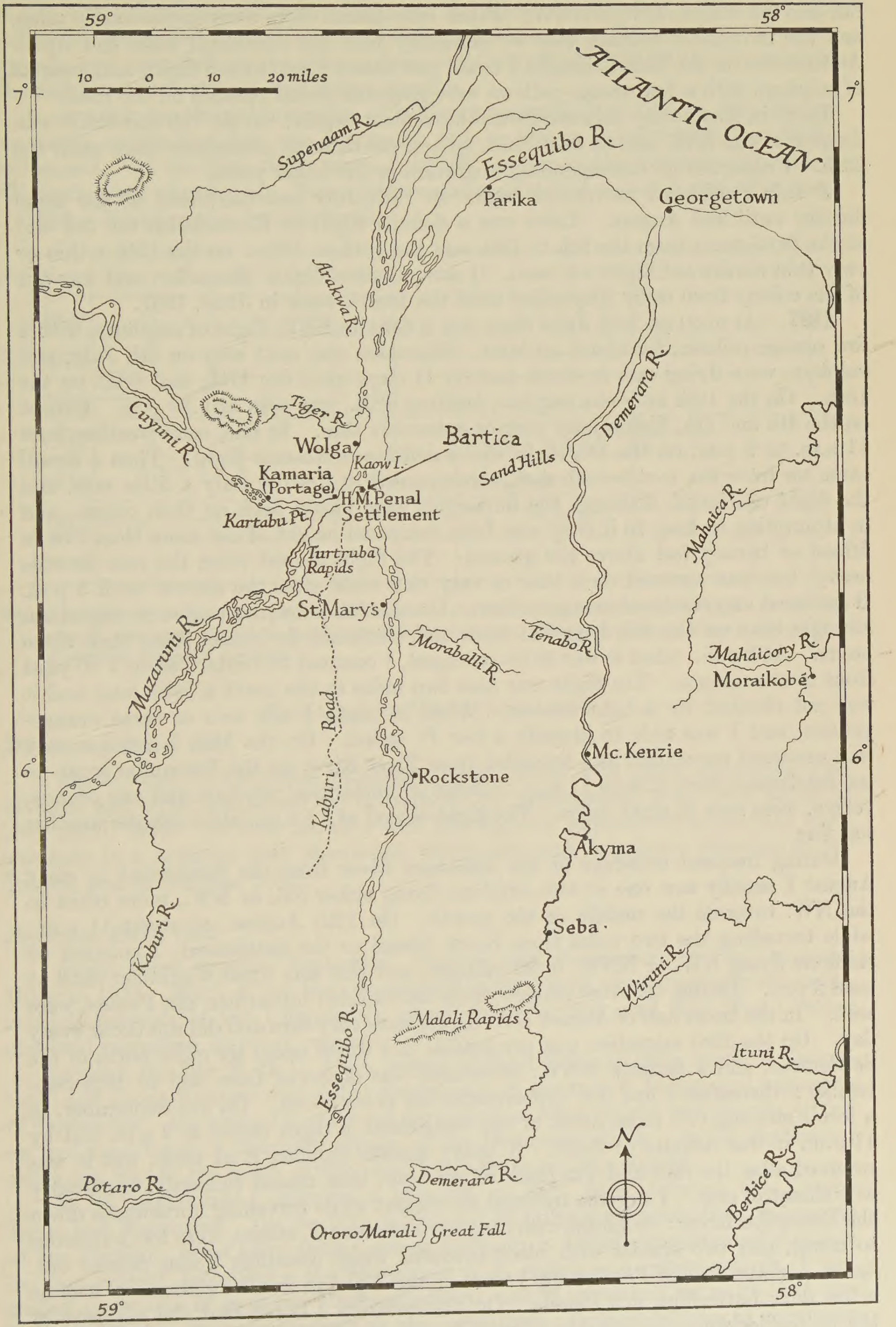

FIG. 1.—British Guiana, showing the localities mentioned.

together. Definite migration continued all through February, and was noted on 5th, 8th and 9th March, always NNW. From 14th March there were unseasonable rains, and the movement became very or extremely thin but continued until 2nd April. At Kamaria on the 12th I thought I could just detect a northward flight, and swarms of sulphurs with a few orange-yellows were gathered round puddles on the road.

Early in May a very thin southward movement began : on the 7th and 8th it was definite to the ESE. and so continued, sometimes definite, sometimes thin, until the 25th. I observed no corresponding migration in five other years.

A thin southward movement began on 12th July and continued at the same density until 2nd August. There was a definite flight at Kamaria on the 3rd and at the Settlement from the 9th to 13th and the 16th to 18th : on the 15th a thin or very thin northward flight was seen. I saw no more flights thereafter, and was out of the colony from early November until the fourth week in June, 1937.

1937.—At noon on 24th June there was a definite ENE. flight of sulphurs, with a few orange-yellows, for about an hour. Migration was next seen on 4th July, and sulphurs were flying east or south-east on 11 days until the 17th, and SSE. on the 18th. On the 19th only one sulphur, heading SSE., was seen at 4.30 p.m. Except on the 4th and 8th, flights were very or extremely thin. In fine, calm weather from 11 a.m. to 2 p.m. on the 4th there was a definite south-east flight. Then a squall came up from the south-south-east, accompanied at first by only a little rain, and the flight continued, although the butterflies were blown back on their course, and in attempting to keep to it they rose from the usual height of not more than five to fifteen or twenty feet above the ground. The flight ceased when the rain became heavy, but was resumed on a thin or very thin scale after the shower until 3 p.m. It included an occasional orange-yellow. On the 8th a definite eastward migration, stronger than on the 4th, began at noon and continued for rather more than three hours. At 2 p.m., when it was at its strongest, I counted 38 butterflies on a 40-yard front in one minute. The flight was seen two miles to the north a little later and it was not checked by a light shower. When it began I saw two or three orange-yellows, and I was able to identify a few *P. statira*. On the 16th I noted a very thin eastward movement as I travelled from Tiger River on the Essequibo south to the Settlement from 9.25 to 11 a.m. : about 50 butterflies, sulphurs and one orange-yellow, were seen in eight miles. The flight ceased at 11 a.m., although the weather was fine.

During frequent crossings of the Mazaruni River from the Settlement in early August I usually saw one or two sulphurs flying either SE. or NW., more often to the NW. towards the middle of the month. On 12th August, at about 11 a.m., while travelling the two miles from Kaow Island to the Settlement, I counted 60 sulphurs flying NW. or NNW. in 20 minutes, and this thin flight continued until at least 2 p.m. During the river journey three unidentified butterflies, not Pierids, were seen. In the latter half of August NW. flights were very thin and did not occur every day. On the 23rd migration was perceptible in a forest camp six miles north of the Settlement, and a definite WNW. movement was observed from 2nd to 16th September ; thereafter I had few opportunities for observation. On 6th September, in a forest clearing two miles north of the Settlement, a flight began at 9 a.m. and by 11 a.m. it was definite or thick. A heavy shower stopped it at noon, but it was resumed after the rain and was thick for an hour, then ceased suddenly, apparently at a threat of rain. I saw the resumed movement while travelling northwards down the Essequibo River : sulphurs, including some obvious *P. statira*, were too numerous to count, and two species with black-bordered wings (recalling *Colias croceus* var. *helice*, perhaps female *Phoebis* spp.) were in the flight in small numbers, as well as a few dark butterflies, not Pierids. On this occasion I noted that the majority of the butterflies were rich sulphur in colour, and may well have been *P. eubule*. On the 7th migration was equally strong with some recognisable *P. statira* and a few orange-yellows. On the 15th I observed definite migration in a narrow camp clearing on the Essequibo-Mazaruni watershed near the Barabara River at 9.30 a.m.; the butterflies descended from above the forest roof, crossed the clearing low above the ground, and ascended on the other side to continue their flight above the canopy. The flight was seen at noon in a larger clearing.

A very thin southward migration of sulphurs occurred from 13th to 19th December which, on the first day, was observed a mile or two to the east as well as at the Settlement. At the time there was a light SW. breeze in the morning and a fresh NE. trade wind after 1 p.m. No migration was seen at this season in any other year.

1938.—No migration was observed.

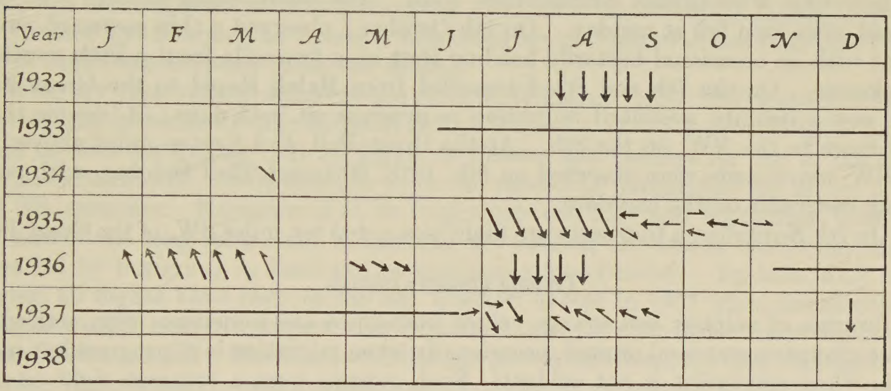

FIG. 2.—Butterfly migrations in British Guiana. Arrows indicate direction of flight in ten day periods, one barb very thin, two barbs thin or stronger. Heavy horizontal lines show periods of absence from the country.

MIGRATION IN OTHER LOCALITIES

Mahaicony River, 1934

I was in camp on the upper Mahaicony River, where with forest alternating with savanna and scrub conditions are favourable for observation, from 18th March to 25th April, 1934. On 26th March a thin SE. flight of sulphurs on a 200-yard front was seen in a savanna near Moraikobé village, the only migration observed in the district, and in the year 1934.

Demerara River, 1935

I spent three months, September, October and November, on the Demerara River in 1935. Much of my time was passed in the forest where butterfly migration is rarely perceptible, but I frequently moved camp by river, and until 22nd October observed migration on every occasion.

A friend, the late M. H. C. Allen, stayed at Sand Hills, 35 miles south of Georgetown and about 20 miles east of the Settlement, at the end of August and beginning of September. He noticed a westward movement of sulphurs and saw swarms settled on wet sand beside a tributary stream of the Demarara River. At the Settlement migration was to the south or SE. until I left there on 29th August.

On 7th September I observed a thin SE. or SSE. flight between the Tenabo River and Mackenzie. On the 20th I travelled 25 miles southwards from the mouth of the Tenabo. Soon after setting out at 9.30 a.m. a definite migration of sulphurs became evident, including a few recognised as *P. statira* and orange-yellows (I estimated about one of each per 1000 butterflies), and it continued for more than five hours to Akyma, 20 miles up river as the crow flies. Beyond Akyma an occasional sulphur was seen, but the movement was barely perceptible. The butterflies crossed the river from east to west, and during the day perhaps two dozen were seen flying in the opposite direction. They flew at the usual height of two to four feet above the tree tops and the water; rarely one rose to eight or ten feet. The majority first appeared in gaps between the taller trees, descended to cross the river, and ascended to continue their flight above the canopy on the far side, following any openings in their path and going round the crowns of tall trees standing above the general level of the forest roof. It was the most impressive flight I had yet seen.

On 27th September I proceeded 15 miles up river to Malali Rapid. A very thin westward movement was noted all the way, with a proportionately greater number of butterflies flying in the opposite direction. Twice I saw a few migrants stop to feed on flowering *Macrolobium acaciaefolium* trees. The flight began at 8.45 a.m. and ceased when rain fell at midday. On 5th October I observed a thin eastward movement with an occasional butterfly heading west on a two-mile front a little south of Mackenzie. On the 7th and 8th I travelled from Malali Rapid to the Great Fall, and saw a definite westward migration in progress on both days; it became thick and more to the NW. on the 8th. At the Great Fall, and for ten miles above, W. or NW. movements were observed on 9th, 12th, 20th and 22nd October, with some flying eastwards on the last date.

On 7th November a thin eastward flight was noted ten miles SW. of the Great Fall.

OTHER OBSERVATIONS

Swarms of sulphur and orange-yellow butterflies are sometimes seen settled in dense groups on wet sand or mud, occasionally when migration is in progress but more often when movement is not evident. Such swarms were a common sight on the Barima River between September and November, 1927, but I did not observe any migration. In July, 1931 I saw similar swarms at Apoteri, Rupununi River, and on the Rewa River, at the riverside and on pads of *Victoria regia* water-lilies in a backwater. On one occasion many were fluttering round a flowering tree. They became abundant on about 4th July and were still abundant when I left for the savannas higher up the Rupununi on the 26th; I detected no movement, and saw no more *Phoebis* butterflies farther up river. In these swarms orange–yellows seem always to be present in proportionately greater numbers than in migrating flights, and in early October, 1936 at the Settlement, a small swarm of about 100 consisted mainly of these butterflies.

I rarely saw migrating butterflies stop to feed: I have given one instance on the Demerara River. At the Settlement on 3rd September, 1937, while a definite flight was still in progress but probably slackening after 3 p.m., a number of *P. statira* and one or two orange-yellows were feeding on *Lantana camara*, and in the late morning on the 14th many sulphurs were on *Bougainvillea*, and others, with two orange-yellows, on *Lantana camara* in the afternoon.

DISCUSSION

Nothing seems to be known of the origin and destination of butterfly migrations in tropical South America, nor of the biological end they serve. A knowledge of the breeding ecology of migratory butterflies might help in solving these problems. The only references to breeding I have found are: R. H. Schomburgk's (1840) statement that he was told by Akawai Indians of the upper Demerara River that the *Phoebis* butterflies he observed migrating deposit eggs on the plants from which they collected caterpillars, and Richard Schomburgk's (1848: 157) that Indians eat the larvae. It is unlikely that the plague of caterpillars reported to Cleare (1929) as dropping from Mora trees (*Mora excelsa*) on the Cuyuni River on 11th October, 1903, were those of *Phoebis*. I had a similar experience on the Issororo River, a tributary of the Pomeroon, in February, 1932. The caterpillars defoliated single trees or small groups of *Mora excelsa*, and presumably left the trees they had defoliated in search of food, since they were not full grown. They were larvae of Heterocera, not Rhopalocera. In North America *Phoebis* larvae (including *P. eubule* and *P. philea*) feed on senna (*Cassia* spp.) and clover (Klots, 1951 : 190–4 ; Scudder, 1889 : 1058) and Scudder also states that in Cuba they are said to feed on other Caesalpiniaceae as well, a family strongly represented in tropical American forests, among other species in British Guiana by several very common forest trees of the genus *Cassia*. It is not even known whether the vast migrating flights of sulphurs seen in British Guiana are bred in the country or elsewhere, and if locally, whether in the forest canopy or in the savannas or in both. R. H. Schomburgk's (1840) supposition that a NE. migration over a nine-mile front, which he saw on the Essequibo River in October, 1838, was crossing from savannas along the Pakaraima Mountains to others between the Berbice and Courantyne Rivers is supported by no other evidence than that their line of flight was between those two areas.

With my observations added to the records, Williams' (1930 : 310) statement that the majority of butterfly migrations in British Guiana are from June to October holds good, as does his finding that all flights of *Phoebis* spp. (except for one to the NE. (R. H. Schomburgk, 1840) referred to in the preceding paragraph) are to the NW. and SE. quarters. Migration is at its height between July and September, towards the end of the long rains, and in the long dry season, the season being sometimes extended by beginning in June and/or continuing into October. In June, July and August all flights have been to the SE. quarter, except in 1937 when the direction changed to NW. early in August. In September and October rather more flights are to the NW. than SE. There is a well-defined period between July and September or October in most years when migration occurs daily, or at least on many days, but in a given locality it can sometimes fail : I could scarcely have failed to observe it in the Bartica district in 1934 and 1938 had there been any flights. Past records (Cleare, 1921, 1929) suggest there are " good " and " bad " years.

Migration is infrequent from November to May, but has now been recorded in every month. Most of the records for this period are of flights observed on one day only in February and March during the short dry season. Strong flights of sulphurs occurred on one day in February, 1914 to the west, and to the east on 18th March, 1919 (Cleare, 1921) and a weak one to the south-east on 26th March, 1934 Flights of *Appias drusilla* Cramer (Pieridae) have also been recorded in the short dry season, one to the south-west on 14th March, 1927 (Cleare, 1929) and one to the north, which continued for three days in April, 1909 (Leechman, 1913 : 137) : both occurred on the coast in the Berbice district. The north-west migration of sulphurs in the Bartica district from 20th January to 2nd April, 1936 had all the characteristics of migration at the normal season in a good year. The nearest approach to movement on such a scale at this time of year is the south-east migration of *Lignyostola crinisus* Cramer (Hesperidae) reported by D. B. Fanshawe at the Settlement : it was on a four-mile front from 15th February to 8th March, 1939, with a break of six days in a wet spell (Williams, 1939). This is the only record of migration in British Guiana published since 1930 that I have been able to find. Flights have not previously been recorded in November, December or January.

Previous May records without exact dates refer to sulphurs. A flight to the east 140 miles inland on the Demerara River in May or June, 1916 " at the beginning of the wet season " (Cleare, 1921) is likely to have occurred in May. Another record from the coast to the west of the Essequibo River is of flights to the south-east reported as a regular phenomenon in May, June and July (Williams, 1917). Since there seem to be no other published records, it is permissible to conclude that the observer saw flights in May, 1916, but that his memory may have been at fault regarding the date in other years. My only May observation was of south-east migration over a period of three weeks. Flights would not be expected to be a common occurrence in this usually rainy month.

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OBSERVATIONS ON THE EGG-LAYING OF SOME BRITISH CADDIS FLIES AND ON CASE-BUILDING BY NEWLY HATCHED LARVAE

By Hilmy M. Hanna*

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Introduction

A few observations have been made on the egg-laying of caddis flies by Silfvenius (1906), Siltala (1907), Wesenberg-Lund (1913), Murphy (1919), Klingstedt (1926), Hora (1930), Kuwayama (1934), Denning (1937) and Badcock (1953).

While there are many published descriptions of the cases of full grown larvae, few attempts have been made to follow the construction of a case from the beginning. The only complete accounts appear to be those of Wesenberg-Lund (1910, 1911) for *Glyphotaelius punctatolineatus* Ritzema and *Phryganea grandis* L. Observations on cases of newly hatched larvae have been made by Walser (1862), Morton (1890), von Linden (1892 and 1898), Struck (1899), Silfvenius (1902, 1904), Siltala (1907), Murphy (1919), Lestage (1921), Uhlmann (1932), Dembowski (1933) and Berg (1938). All these observations are brief and fragmentary. The present work is a detailed study of the construction of the first case by larvae of twelve species of British caddis flies. Observations have also been made on egg-laying, the form of the egg masses and on the hatching of the larvae.

Material and Methods

This work was carried out on *Phryganea grandis*, *P. striata* L., *Limnephilus flavicornis* (F.), *L. lunatus* Curtis, *Potamophylax stellatus* (Curtis), *Drusus annulatus* Stephens, *Notidobia ciliaris* (L.), *Brachycentrus subnubilus* Curtis, *Athripsodes senilis* (Burmeister), *A. cinerea* (Curtis), *Mystacides longicornis* (L.) and *Oecetis lacustris* (Pictet).

The adults were collected in the Reading area, either by means of a Robinson mercury vapour light trap or by sweeping the vegetation. For the study of egg-laying only adults freshly collected in the field were used. They were put in large shallow dishes containing water with stones and plant material projecting above the surface. The process of egg-laying was then observed. Egg masses were transferred to deep dishes containing Reading tap water, sand and plant material; the same materials were provided for each species. Air was bubbled through the water, which was changed once every three days. The time necessary for the development of the eggs at ordinary room temperature was recorded. The newly hatched larvae were watched under a binocular microscope while they constructed their cases. For each species a large number of larvae was studied.

Results and Discussion

Egg-laying

Caddis flies may be divided into the following three groups according to the way in which they lay eggs.

(1) *Egg masses laid on the water surface.*—This method of laying egg masses was observed in the following species: *A. senilis*, *A. cinerea*, *M. longicornis* and *O. lacustris* among the Leptoceridae, and a single species, *N. ciliaris*, from the Serico-

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stomatidae. In each species the female rested on the water surface and the egg mass sank slowly to the bottom. However, three females, one of *N. ciliaris*, one of *A. cinerea* and the other of *M. longicornis*, were seen to crawl under the water and affix their egg masses to stones. Furthermore, a few egg masses of the latter two species were found in the field attached under stones in the water. Silfvenius (1906) also recorded egg masses of some Leptoceridae fixed to objects under water. Kuwayama (1934) reported on two species of this family that laid their egg masses on the surface of the water. Thus, although the females of this family usually lay their eggs on the surface of the water, those of certain species are capable of going beneath the water for this purpose. Klingstedt (1926) observed *Limnephilus decipiens* Kolenati laying its egg masses on the water surface but, as will be shown later, this is not usual in the Limnephilidae.

(2) *Egg masses laid under water.*—I have observed *Phryganea grandis* and *P. striata* from the Phryganeidae and *B. subnubilus* from the Sericostomatidae crawling down vegetation to lay egg masses under the water. The egg mass protruded a little from the tip of the abdomen as the insect crawled, head first, down a stick or a stone under the water surface. An air film surrounded the insect and gave it a silvery appearance. The tip of the abdomen was then bent forward so as to attach the free end of the egg mass to the stems or the stones. The egg mass was then pulled out from the genital pocket. In *P. grandis* one specimen only laid an egg mass in the form of the wreath which, from published accounts, appears to be typical for this species, and this was achieved by bringing the end of the egg cord round to the point where the beginning had been attached. All the other females belonging to both species of *Phryganea* laid only small incomplete egg masses which were not large enough to fasten into a wreath. Immediately after laying the insect crawled out of the water and shortly afterwards died ; no second oviposition has been observed.

This method of egg-laying has been recorded by many workers in Trichoptera and in other insect orders by Percival and Whitehead (1928), Fisher (1932) and Matheson and Crosby (1912).

(3) *Egg masses laid above the water surface.*—This would appear to be the normal habit in the Limnephilidae. I have observed *L. flavicornis* and *L. lunatus* laying their egg masses above the water surface. When ready to oviposit, the insect held on to some suitable vegetation and the egg mass protruded at the tip of the abdomen, The abdomen was bent forward and the tip of the egg-mass was stuck to the vegetation. The complete egg mass was then drawn out of the genital pocket and stuck firmly down. In nature egg masses of these two species were found a few centimetres above the water surface. The egg masses of *Glyphotaelius pellucidus* (Retzius) and of *Potamophylax stellatus* were found on the aerial parts of aquatic vegetation.

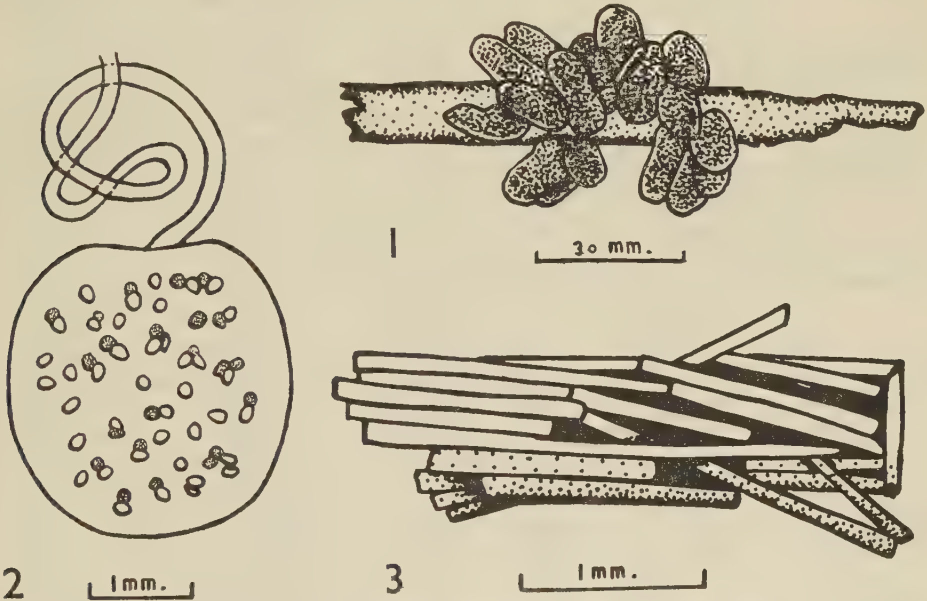
The eggs of Limnephilidae have been found on vegetation above the surface of the water by McLachlan (1879), Silfvenius (1906), Vorhies (1909) and Wesenberg-Lund (1908, 1910 and 1913).

Eggs and hatching

The single complete egg mass of *Phryganea grandis* was in the form of a wreath. The green eggs were arranged in 48 rings. When first laid the cord was rather opaque and the eggs very close to each other. With the absorption of water it became transparent, the eggs becoming widely separated. All the egg masses of *P. striata* were incomplete.

The egg masses of *L. flavicornis*, *L. lunatus*, *Potamophylax stellatus*, *D. annulatus* and *A. senilis* were colourless, domed and circular. The eggs of *L. flavicornis* and *D. annulatus* were scattered irregularly through the egg mass, whereas those of *L. lunatus* and *P. stellatus* were arranged in concentric rings. The eggs of these four species were colourless. The eggs of *A. senilis* were arranged in longitudinal rows and were green.

The colourless egg masses of *N. ciliaris* were formed of two elongated rounded halves, folded on each other and joined at one end. The free end was protruded first from the tip of the abdomen. One of the two halves was usually longer than the other and each was broadest at the point of attachment and tapered gradually towards the free end. The egg masses had a depression on the larger half near the point of attachment. Both halves had a number of notches at the edge and a number of transverse furrows on the surface. In one of the egg masses the two halves lay nearly at right angles and were nearly equal; both the depression and furrows were lacking. In another instance an egg mass was formed only of one part. In this the jelly was of a firmer nature and more compact than in any other egg mass. The colourless eggs were arranged in transverse curved rows.



FIGS. 1–3.—(1) Egg masses of *Brachycentrus subnubilus* Curtis; (2) egg mass of *Oecetis lacustris* (Pictet); (3) case of newly hatched larva of *Phryganea grandis* L.

The elongate, flat, rounded egg masses of *B. subnubilus* were found in large numbers attached to the bordering vegetation of the Whitewater River and were submerged a few centimetres beneath the water surface, usually grouped together in large numbers over a small area (fig. 1). In them the jelly was colourless and the eggs, which had no special arrangement in the mass, were light green.

The egg masses of *A. cinerea* were spherical and had colourless jelly. The eggs were green and had no special arrangement in the egg mass.

The circular flattened egg masses of *M. longicornis* had colourless jelly. The green eggs were arranged in sinuous rows, 7–8 near the edge and 3–4 centrally. The rows were surrounded by a creamy sheath.

The spherical egg masses of *O. lacustris* had a small notch from which came a filament (fig. 2), measuring up to 14 mm. in length. The jelly was colourless or yellowish-green. The green eggs had no special arrangement in the egg mass. There appears to be no published description of such a filament attached to the egg mass of any species of caddis fly. In water it was seen to twist round submerged stems; when the mass sank to the bottom the filament became covered with sand grains. From these observations it seems reasonable to suggest that the filament may be used as an anchor for the egg mass.

The dimensions of the egg mass, the number of eggs, their shape and dimensions and the period necessary for hatching are recorded in the following table:

	Egg masses		Eggs		Period of hatching (days)
Species	Size (mm.)	No. of eggs	Shape	Size (mm.)	
P. grandis .	37	607	spherical	0·62–0·71	15–18
P. striata .	incomplete egg masses		spherical	0·58–0·67	14–16
L. flavicornis .	8·2–8·5	317–369	spherical	0·32–0·36	18–20 (above water) 14–16 (in water)
L. lunatus .	7–7·6	298–359	spherical	0·3–0·38	18–20 (above water)
	.	.	oval	0·32–0·38 long	15–18 (in water)
	.	.	.	0·25–0·28 wide	.
P. stellatus .	9·1–9·7	344–371	spherical	0·37–0·39	13–17
D. annulatus .	14	240	oval	0·34–0·38 long	.
	.	.	.	0·27–0·29 wide	.
N. ciliaris .	larger half: 2·6–7·2 long	92–323	oval	0·28–0·31 long	18–22
	3–5·9 wide	.	.	0·19–0·23 wide	.
B. subnubilus .	6·8–11·9 long	561–702	elongate and tapering at one end	0·23–0·32 long	12–18
	4·1–5·9 wide	.		0·18–0·23 wide	.
A. senilis .	5–5·5	173–264	spherical	0·2–0·22	10–14
A. cinerea .	3·5–3·8	259–281	spherical	0·2–0·25	.
	.	.	oval	0·25–0·28 long	.
	.	.	.	0·18–0·20 wide	.
M. longicornis .	5·2–6·5	218–257	spherical	0·25–0·28	11–14
O. lacustris .	2·5–4·1	35–60	oval	0·25–0·39 long	10–13
	.	.	.	0·20–0·22 wide	.

Case-building

The newly hatched larvae of the twelve species examined constructed initial loose cases after leaving the egg mass, and then added the building materials to the anterior end in a more compact way. When a good deal of the case had been built, the larva inside reversed itself and cut away the initial part, and then continued to add material at the anterior end.

In the Phryganeidae the larvae of *P. grandis* and *P. striata* constructed non-spiral cases. The spiral fashion of building was not adopted until the third day by the former and the second day by the latter species. The larva of *P. grandis* built the first ring of its case as a square and then added short lengths of *Ceratophyllum* anterior to this (fig. 3). Although provided with the same materials as *P. grandis*, the larvae of *P. striata* started to build cases as simple tubes from detritus.

Siltala (1907) described the first cases of *P. striata* as built of jelly, moss leaves or pieces of reed. Only the cases built of reed were spiral. Wesenberg-Lund (1911) described how the newly hatched larvae of *P. grandis* built loose cases of decayed vegetable matter.

In the Limnephilidae both *L. flavicornis* and *L. lunatus* used the same method of case-building right through larval life, with some exceptions in the second species. The cases of the former species were built of a mixture of *Ceratophyllum*, dead leaves and decaying vegetable matter and, occasionally, sand grains. The material was arranged transversely and irregularly. In *L. lunatus* some of the cases were entirely constructed of fine sand grains ; others were built of dead leaves or pieces of *Ceratophyllum* arranged longitudinally, and some of a mixture of these materials. In *L. lunatus* some of the early cases, however, were built of detritus and were thus different from later ones. In *Potamophylax stellatus* and *D. annulatus* the cases of newly hatched larvae were quite different from those of later stadia. The first case of the former species was a simple cylindrical tube of fine sand grains. The larva then constructed a slightly curved case at the anterior end of the initial case, and when this was completed it started to use small pieces of bark together with sand grains. On about the ninth day some were built entirely of bark with a stick attached along the whole length, as in the cases of *Anabolia* and *Halesus*. The first cases of *D. annulatus* were cylindrical and slightly curved. By the fifth day, they assumed the curved tapered form of later stadia.

In the Sericostomatidae, *N. ciliaris* constructed cylindrical cases of fine sand grains. Many had a bulky ring at the posterior end. A curved case, the same width at both ends, was then built at the anterior end. When the initial case was cut away, the posterior opening was partially closed by fine sand grains and a silken secretion. After a period of almost three weeks the cases became curved and conical and the larva secreted a membrane at the posterior end with a circular hole in the middle. The larvae of *B. subnubilus* constructed cylindrical cases of detritus found on the egg masses. They continued to add detritus at the anterior end and the square form of the cases started to appear. They were therefore cylindrical posteriorly and square anteriorly. The larva continued to add detritus and small bits of dead leaves at the anterior end. By the second or third day it cut away the cylindrical part. The cases were then square in cross section and the same width at both ends. Plant materials arranged transversely were then added, and in about a week the case was built of *Ceratophyllum* and dead leaves and had a membrane at the posterior end with a central hole.

In the Leptoceridae the first cases were simple tubes built of detritus in *A. senilis*, or barrel-shaped structures built of detritus and a few sand grains in *A. cinerea*. The newly hatched larvae of *M. longicornis* and *O. lacustris* built cylindrical tubes of fine sand grains. The larvae of all four species then built, at the anterior end, a curved cylindrical case, the same width at both ends and continued to add material at the anterior end so that eventually the curved tapered cases of later stadia were built. Thus, in these species of Leptoceridae the first cases are different from those of later stadia. This has also been shown for *Triaenodes bicolor* (Curt.) by Siltala (1907), Lestage (1921) and Berg (1938).

From the above observations it is clear that the first case built by a newly hatched larva is usually different in form from that typical of the older larva.

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A HORMONAL THEORY OF THE MECHANISM OF WING POLYMORPHISM IN HETEROPTERA

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Alary polymorphism, more correctly termed pterygo-polymorphism, the occurrence of various wing forms or morphs in the same species, is widespread in the Heteroptera, occurring commonly in all the major groups except the Pentatomoidea and the Hydrocorisae. In the latter group the fore wings, which retain air when submerged, are fully developed even when the power of flight is lost, e.g. *Ilyocoris*, and a reduction in their size only occurs when an efficient plastron has been evolved, as in *Aphelocheirus*. The fully-winged morph is commonly referred to as the macropter and the short-winged variously as the brachypter, micropter or apter, depending on the degree of the reduction of the fore wing ; these latter terms have been given approximate definitions by Southwood & Leston (1959).

Alary polymorphism has been studied by many workers, most of whom have attempted, without success, to find some all-embracing genetic explanation (Poisson, 1924 ; Ekblom, 1941), while Teyrovsky (1920) suggested that the short-winged morph was the result of a shortened life-cycle. Wigglesworth (1954, 1960) has suggested that many forms of polymorphism may be due to hormones acting directly or via the cytoplasm on the gene system in the nucleus. The present note attempts to review the information available on alary polymorphism in the Heteroptera in the light of this theory.

Certain definite information is available associating the one or other morph with higher altitudes (Stehlik, 1952 ; Hynes, 1955) or colder temperatures (*e.g.* Forster, 1954). Recently Brinkhurst (1958, 1960) has studied the phenomenon in detail in the Gerroidea, and he has not only demonstrated its biological significance in the different species, but has suggested that, although a different genetic constitution may account for some of the cases of polymorphism, in many it seems that an environmental factor is responsible for switching the phenotype to one or other of the morphs. Brinkhurst (1959) postulates that temperature might be such an environmental factor and describes an experiment in which the raising of the temperature led to the production of the long-winged morph when under colder but normal conditions, short-winged adults are usually produced.

Now short-wingedness is really a juvenile character (Cousin, 1935 ; Sellier, 1949 ; Wigglesworth, 1954), and is likely to arise through the change in the concentration of the juvenile hormone which is necessary for the production of the long-winged adult. This change could be brought about in either of two ways :—

(1) by excessive influence of the juvenile hormone, leading to juvenile characters in the adult—*metathetely*.

(2) by depression of the influence of the juvenile hormone (and thus loss of the prothoracic glands and failure of the moulting hormone), leading to adult characters in the larva—*prothetely*.

The problem arises of distinguishing between the former, production of an adult with larval characters, which could perhaps be called neoteny, and the latter, a larva with adult characters, which is a condition homologous with paedogenesis. It is suggested that this can only be done by a consideration of the number of instars passed through ; when after the normal number of instars, a morph with some juvenile characters is produced, this may be considered as metathetely, a juvenile adult. If, however, there is a reduction in the number of moults, then the morph produced is an extreme example of prothetely. Such a differentiation may appear artificial, but it does have the important distinction, in the present theory, that the former results from a lengthening of the period of influence of the juvenile hormone and the latter from a reduction in this period.

Several workers (Pruthi, 1924 ; Thomas, 1932 ; Nagel, 1934) have shown that metathetely is associated with cold conditions and prothetely with hot, and Wigglesworth (1952) has demonstrated these temperature effects experimentally in the larvae of the heteropteran *Rhodnius prolixus* Stål.

In many groups of insects brachypterism is associated with the loss of ocelli (Kalmus, 1945) ; in the Heteroptera this association is complete only in the Microphysidae. All Miridae and Tingidae, whether short-winged or not, lack ocelli, whereas these organs are present in the short-winged individuals of other families. However, a careful examination of specimens of several bugs has shown that at least in some species—*Ischnodemus sabuleti* (Fall.) and *Mesovelia furcata* (Mulsant and Rey)—the ocelli are larger and a brighter red in the fully-winged than in shorter-winged individuals. Now it seems that dorsal ocelli are an adult character and their association with fully developed wings is purely the association of two adult characters controlled by the same hormonal condition ; indeed Pflugfelder (1939) obtained adult *Dixippus* (Phasmida) with ocelli when under experimental conditions the normal somewhat larval and ocelli-less " adults " underwent additional moults.

(1) *Short-wings, an Aspect of Metathetely*

Thus in those Heteroptera where higher altitudes or colder conditions are associated with brachypterism, the low temperature has acted on the hormone balance and led to the production of metathetelous adults. The action may simply be due to the longer time spent in the larval state and therefore the longer the period under the influence of the juvenile hormone, as was demonstrated by Sellier (1949) in *Gryllus*. Thus this explanation for mountain brachypterism is the direct opposite to that of Teyrovsky (1920).

This type of brachypterism is found in the Gerroidea where brachypterism is associated with higher altitudes (Teyrovsky, 1920 ; Stehlik, 1952 ; Hynes, 1955), colder regions (Förster, 1954 ; Brinkhurst, 1960) and, in many bivoltine species, with the first generation (Brinkhurst, 1958, 1959, 1960). This first generation is in the larval state in May and June when the temperatures are considerably lower than those experienced by the second generation larvae in July and August, and, as Müller (1954) has found with Homoptera, these spring and summer temperatures are sufficiently different to produce considerable variations in growth. Brinkhurst's (1959) demonstration of the production of macropterous adults of *Gerris odontogaster* (Zett.) in the first generation by raising the temperature to which the eggs are subjected whilst in the female, can be regarded as an experimental confirmation of the significant role of temperature.

Mountain brachypterism also occurs in *Nabis ferus* (L.) (Nabidae), *Bryocoris pteridis* (Fall.) (Miridae) and *Trapezonotus* spp. (Lygaeidae) (Stehlik, 1952 ; Southwood, *unpub.*) ; whilst in *Neides tipularius* (L.) (Berytinidae) hot springs and summers are said to be associated with the production of fully-winged forms (Hertel, 1955). Woodroffe (1960) records that in the exceptionally hot summer of 1959, the proportion of macropters in various normally brachypterous species was above normal. In various Tingidae, e.g. *Acalypta*, *Lasiacantha* and *Camplyosteira*, the "rare" macroptera are only found in warm localities and never on the northern fringes of their range.

(2) *Short Wings, an Aspect of Prothetely*

Dolichonabis limbatus (Dahl.) (Nabidae) has but four larval instars (Southwood and Fewkes, 1961), whereas most Heteroptera have five ; furthermore Stehlik (1952) has observed that the long-winged morph occurs most frequently under cold mountainous conditions. Thus it seems that *Dolichonabis* adults are normally a case of " paedogenesis ", or extreme prothetely, and only under especially cold conditions does the normal hormone condition obtain. Frick (1949) and others have found that at least some *Microvelia* spp. have four or five instars ; the " adults " produced in the former condition are always apterous (and usually always males) and must be considered to be paedogenetic. The abnormally large genital capsules of *Dolichonabis* and *Microvelia* larva are a further indication of their prothetelous condition—even before the last instar. Frick (1949) found that brachypterous adults also occurred after five larval instars—on the present hypothesis it is suggested that these were adults showing metathetely due to cold conditions. Female Coccidae have one fewer moult than the males and retain many larval characters. They are generally described as neotenous, but in view of the reduction in the number of moults they must be considered rather as larvae with adult characters, *i.e.* paedogenetic, than as adults with larval characters (neotenous). The same is probably true of *Dixippus*.

In all the cases discussed above there is little definite association of sex and wing morphs, but in many Miridae and all Microphysidae the male is generally fully winged and the female always or usually brachypterous. In some Heteroptera the development of the males is usually faster than that of the females (Giles, 1959), thus the female larvae are under the action of the juvenile hormone for a longer period and it may be that even in these species female brachypterism is an expression of metathetely rather than a genetic condition. However, in a few species, e.g. *Mecomma ambulans* (Fall.) (Stehlik, 1952 ; Carvalho and Southwood, 1955), the rare macropters occur in colder and mountainous regions ; this is not covered by the present hypothesis, but the hormone level might well be disturbed by factors other than temperature.

Wigglesworth (1952) has remarked how, as with the determination of sex, the finely adjusted hormone balance between larval and adult morphs is an " all or none " reaction, producing either one morph or the other, intermediates being rare. The same applies to alary polymorphism in the male of the ichneumonid *Gelis* (Salt, 1952) and in most cases in Heteroptera, the great majority of adults exhibiting one of two fairly definite wing sizes. However, in some bugs, such as the Lygaeid *Scolopostethus thomsoni* Reuter all gradations between the fully winged and the micropterous condition commonly occur ; the underlying hormone changes in such cases would be of exceptional interest. It is realised, of course, that in nature mixed populations of long and short-winged individuals sometimes occur. It seems more probable that the wing form of some of the individuals is entirely determined by their genotype, whilst in others the genetic make-up allows a plasticity of form, the final morph being determined by the environment through the action of hormones. It is clear that an experimental study on alary polymorphism in Heteroptera using the techniques of Wigglesworth (1954) and others would not only increase our understanding of this phenomenon, but might lead to a further understanding of the nature of the hormone balance in insects.

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BLAESOXIPHA BINODOSA CURRAN (DIPTERA : CALLIPHORIDAE) PARASITISING *CATALOIPUS OBERTHURI* I. BOLIVAR (ORTHOPTERA : ACRIDIDAE)

By R. F. Chapman

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During April, May and June, 1956, while I was working in the Rukwa Valley, Tanganyika Territory, a number of adults of the grasshopper *Cataloipus oberthuri* I. Bolivar were found to be parasitised by the larvae of *Blaesoxipha binodosa* Curran (?=*anceps* Villeneuve). A total of 114 *C. oberthuri* were examined and 15 per cent. of these were parasitised, the proportion being similar in both sexes. It is, however, probable that the percentage parasitised was exaggerated by the parasitised specimens being sick and so more readily caught than healthy individuals.

In 23 parasitised grasshoppers the number of fly larvae varied from one to eleven, while in one female 26 larvae were found. The parasites often caused the death of the host, but even before this the development of the ovaries in females was reduced when compared with non-parasitised specimens collected at the same time (Table I), and there was a highly significant difference between the numbers of parasitised and unparasitised specimens which had the ovaries completely undeveloped ($\chi^2 = 17{\cdot}4$, $0{\cdot}001 > p$). In some cases, however, well-developed eggs were present in the ovaries or oviducts of parasitised females.

Table I.—*The development of eggs in the ovaries of parasitised and non-parasitised female* Cataloipus (*Expressed as percentages in each size group*)

	Parasitised	Non-parasitised
Number in sample	18	46
No development	61	11
Size of eggs (mm.) :		
1·0	0	2
2·0	6	11
3·0	0	30
4·0	6	24
5·0	17	17
In oviducts	11	4

During the same period, April to June, and again in December, other species of grasshopper were examined but no parasites were found. The species examined, which included all the commoner Catantopinae found in the same habitat as *Cataloipus*, were (April to June) *Afroxyrrhepes procera* (Burmeister) (84), *Catantops melanostictus* Schaum (62), *Catantops axillaris* (Thunberg) (50) ; and (in December) *Eyprepocnemis plorans* (Charpentier) (71), *Tylotropidius speciosus* (Walker) (31), *Phaeocatantops decoratus* (Gerstaecker) (21). In addition to these, over 250 specimens of the Red Locust, *Nomadacris septemfasciata* (Serville), and numbers of other grasshoppers were examined in every month during which they were adult from March, 1955 to December, 1956. No *Blaesoxipha* larvae were ever found in them, although other dipterous parasites were present. Thus, in the Rukwa Valley, *B. binodosa* appeared to be specific to *C. oberthuri*. There is, apparently, no other published information on host preferences in this species.

The fly larvae were seen to leave the host by way of the tympanum and, in general, they pupated immediately, the flies emerging 7–11 days later when kept at about

25° C. However, all the larvae did not pupate immediately and many were kept alive on dry cotton wool in specimen tubes. Thus in September many of the larvae taken in May were still alive, while any of the puparia which had not already hatched were dead. The larvae were contracted to less than half their normal lengths, but they became active immediately on being disturbed.

From September onwards the surviving larvae were subjected to a variety of treatments which led to their pupation. Some were placed on moist cotton wool, others on fresh dry cotton wool, in dry soil or in empty tubes and in all cases some individuals pupated while others remained as larvae. One larva which had not been disturbed at all pupated at the end of September. From these puparia the adult flies emerged after 10 or 11 days in September, October and November. Others of the larvae did not pupate and one on dry cotton wool was still alive in February, 1957, nine months after it had been found in the host grasshopper. Mellanby (1938) has recorded a comparable termination of diapause, by placing the larvae in empty tubes, in the larvae of *Lucilia sericata* Meigen.

By this method he was able to end diapause in practically every case, but this was not true of *Blaesoxipha*. Another point of difference is that Mellanby stressed the lack of contact in the empty tube as the stimulus leading to the ending of diapause, but in *Blaesoxipha* pupation occurred in some instances when the larva had burrowed into fresh earth or cotton wool. This may suggest that any shock stimulus, provided here by the transfer from one tube to another, could suffice to end the diapause although it must be noted that a number of larvae failed to pupate after this treatment.

These laboratory observations are of some interest since they suggest that this species might be able to persist as larvae in the field over the dry season, which in the Rukwa is from May until October. *Cataloipus oberthuri* is only found as an adult grasshopper for a few months of the year, from March to June, and the eggs, laid at this time, remain in diapause until the following wet season (Chapman and Robertson, 1958). Hence it is available as a host for *Blaesoxipha* only during this period, or possibly from January if nymphs are also parasitised. If *B. binodosa* is confined to *Cataloipus* some mechanism for surviving the dry season, such as a larval diapause, must operate, although larvae which did enter diapause were found throughout the adult season of *Cataloipus* and not only at the end as might have been expected. It is known that in temperate regions *Blaesoxipha lineata* Fallén may overwinter in the larval form (Clausen, 1940).

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POST-TENERAL DEVELOPMENT OF THE THORACIC MUSCULATURE IN TSETSE FLIES

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Introduction

In most studies of tsetse bionomics a distinction is made between flies which have fed and flies which have not yet had their first blood meal, the latter being termed " teneral ", the former " non-teneral ". Criteria are available for diagnosis of the teneral state (the absence of blood meal remnants in the gut, the possibility of causing eversion of the ptilinum by pressure on the head capsule and the characteristic softness of the thorax (Buxton, 1955)), but little is known of the details of the process of deteneralisation. It seemed possible that a change in the degree of hardening of the cuticle might be involved (*see* Jackson, 1949), but a preliminary histological study of the thoracic cuticle failed to reveal such a change. It was subsequently noted that the residual (= non-fatty) dry weight of the non-teneral thorax was much greater than that of the teneral, and it was thought that post-teneral development of thoracic musculature might account for the increased firmness of the thorax.

Methods

The relation between the size of flies (thoracic surface) and the residual dry weight of thorax, head, wings and legs (henceforth referred to as thoracic RDW) was determined for teneral and non-teneral individuals of both sexes ; the details of the techniques have been described elsewhere (Bursell, 1959, 1960). For histological examination flies were fixed in alcoholic Bouin, imbedded in paraffin wax and cut at 7 μ ; the sections were stained with eosin and haematoxylin.

Results

Figure 1 shows the relation between thoracic surface and thoracic RDW in teneral and non-teneral *G. swynnertoni* Austen collected at Shinyanga in February and March 1959. Thoracic RDW is clearly much greater in non-teneral than in teneral flies ; in males the difference is about 2 mg., in females, 3 mg.

The figure illustrates also a difference between teneral males and females noted in a previous publication (Bursell, 1960) namely that for a given weight the thoracic surface of teneral females is about 13 per cent. greater than that of males. The implications of this difference were not appreciated at the time, but it is clearly related to, and may be said to foreshadow, the much greater weight increment characteristic of females.

The thorax makes up about two-thirds of the total fresh weight of the fragment weighed, and it seemed likely that an increase in the bulk of thoracic musculature could account both for the increase in dry weight and for the increase in firmness of the non-teneral thorax. To test this possibility a pair of flies were selected as nearly as possible the same size, one teneral and one non-teneral ; they were fixed, imbedded, cut and stained together and the resulting sections examined. Corresponding parts of the thorax could be selected with reference to some easily identifiable points, such as the proventricular origin of the mid gut, and figure 2 shows two such cross sections. Only the longitudinal flight muscles have been included—with oblique and dorsoventral musculature slight differences in the plane of cutting would invalidate the comparison. The difference in the cross-sectional area of these flight muscles in teneral and non-teneral flies is very striking, and there can be little doubt that one of the most important factors involved in the process of deteneralisation is an increase of the thoracic flight musculature. In view of this it is not surprising that tsetse flies tend to be inactive during the early part of their lives (Jackson, 1946, 1948), nor that the flight of tenerals is " less noisy and determined " than that of non-tenerals (Jackson, 1933).

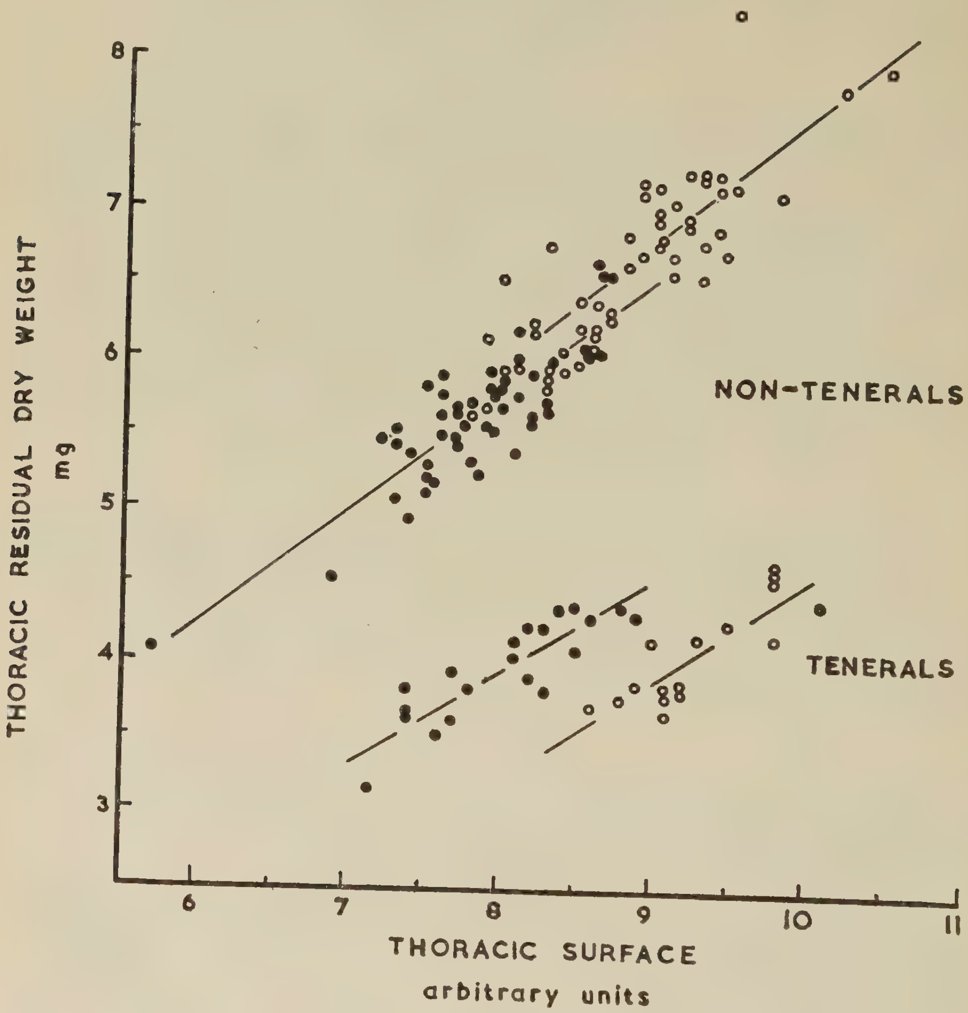

FIG. 1.—The relation between thoracic surface and thoracic RDW in teneral and non-teneral *G. swynnertoni*. The lines have been calculated from the formulae of regression. ● =males; ○ =females.

Occasionally flies are caught which cannot readily be assigned to teneral or non-teneral categories; it has for many years been the practice at the Shinyanga Tsetse Research Laboratories to record such individuals as " doubtful ".[1] They are non-teneral in general appearance, often with visible remnants of a blood meal in the abdomen, but still have something of the characteristic soft feel of the teneral. Such flies are represented in the present investigation by occasional individuals (not included in fig. 1) whose thoracic RDW is intermediate between the teneral and the non-teneral levels; their occurrence is a reflection of the fact that the growth of thoracic musculature is a gradual process extending over a period of days (*see below*).

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[1] The existence of this " doubtful " category was first recognised by Dr. E. Burtt, formerly of E.A.T.R.O.

Figure 1 illustrates that a great deal of the variance of RDW is unaccounted for by the regression with size; two additional sources of variance have, in fact, been identified. In the first place the RDW of the thorax has been found to decrease by more than half a milligram towards the end of the hunger cycle (Bursell, 1958*b*). This suggests that substantial quantities of non-fatty food reserves occur in the thorax of the tsetse fly; their chemical nature is as yet undetermined, but fluctuations in the amount of such reserves will obviously contribute to the variance of thoracic RDW.

In addition it has been found that there is a gradual increase in the RDW of the thorax with age. The quantitative aspects of this increase have been studied in samples of *G. swynnertoni* collected in the field. Immediately after capture a narrow (0·5 mm.) strip of the trailing edge of the wing was cut off with spring scissors (the cutting edges coated with a film of glycerine to prevent loss of the fine membrane) and the strips were mounted in glycerine for subsequent determination of wing fray. The flies were then placed singly in 3 × 1 inch glass tubes covered at one end by mosquito gauze, and starved to death at high relative humidities in order to exhaust the above-mentioned non-fatty reserves, after which thoraxic RDW was determined. Regressions of weight against thoracic surface were calculated for each of the wing-fray categories and comparisons between samples made at a given level of size. These size-specific dry weights are shown in Table I against the corresponding wing fray categories (Jackson, 1946). It is clear that there is a progressive increase in thoracic RDW with age, and, for samples comprising flies of various ages this will constitute a further source of variation. The nature of the substance involved has not been determined, but it seems possible that the phenomenon may represent the accumulation of some metabolic end product.

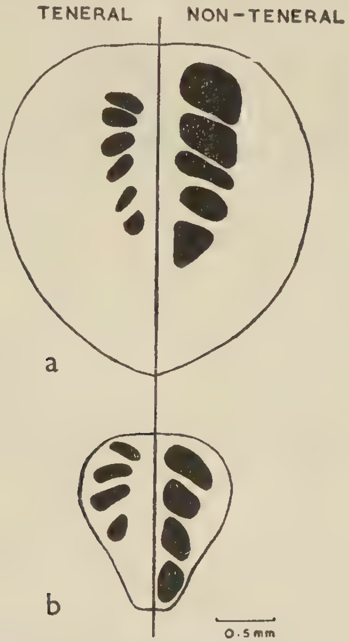

Fig. 2.—Sections through corresponding parts of the thorax of teneral and non-teneral males of *G. swynnertoni*, drawn with a camera lucida.

Table I.—*The size specific residual dry weight of the thorax of male* G. swynnertoni *starved to death at high humidities. Thoracic surface* 7·55 (*arbitrary units*)

Wingfray	Thoracic RDW (mg.)	Standard error	N
1	5·76	0·084	14
2	5·94	0·075	16
3	6·00	0·103	15
4–6	6·16	0·144	10

In this connection it may be noted that the regression lines shown in figure 1 indicate that for a given size the thorax of males is slightly lighter than that of females. From the corresponding formulae the significance of this difference can be established: for a thoracic surface of 8·336 the female RDW is 6·234 ± 0·056 and the male RDW 5·999 ± 0·047; t is therefore $0{\cdot}235/0{\cdot}0731 = 3{\cdot}2$ and $P < 0{\cdot}01$. This difference is probably associated with the longer mean life of females (*see* Jackson, 1944)—the sample of females would be older than that of males and, since the thoracic RDW increases with age, heavier.

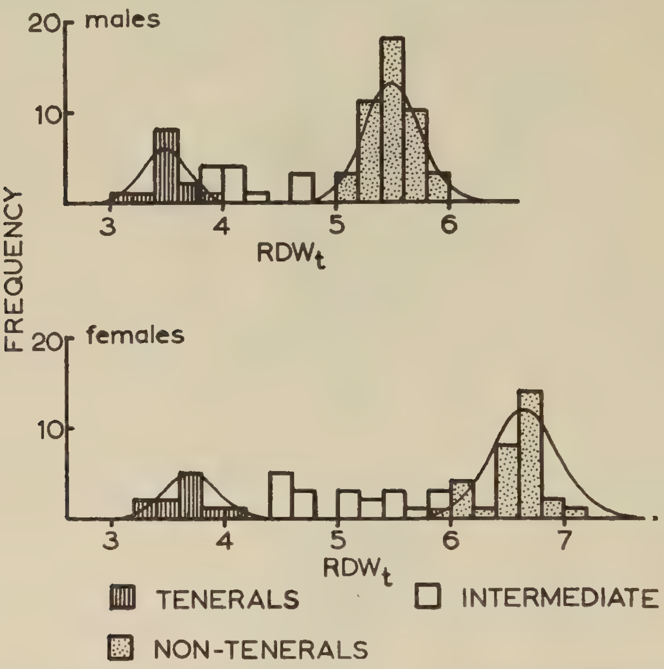

Fig. 3.—Frequency distributions of the size-specific residual dry weight (RDW) of the thorax of male and female *G. swynnertoni* captured on a bait animal. (For further explanation, *see text.*)

Some collections were made in an attempt to determine how long the process of muscular development takes under natural conditions. For this purpose a stationary bait animal was used, and only flies which were observed to probe were included in the analysis. Accurate estimates of the coefficient of regression of RDW on size were available for large samples of *G. swynnertoni* collected in the course of 1958. Using the mean value of 0·900 ± 0·035 so obtained, the RDW's of individual probing flies were corrected to specified levels of thoracic surface (8·0 for males and 9·0 for females) and the frequency distributions are plotted as histograms in figure 3. Estimates were available of the variance of thoracic RDW for teneral flies emerged in the laboratory, and for old non-teneral flies of both sexes (the standard deviation of male and female tenerals is 0·21 and 0·24 mg. and of male and female old non-tenerals 0·24 and 0·30 mg. respectively). Using these, it was possible to fit the expected distribution of these two classes of flies and such normal curves have been super-posed on the histograms. In this way some idea can be obtained of the proportion of the total catch which should be assigned to teneral and non-teneral categories. The results show that an appreciable percentage of flies have thoracic RDW's intermediate between the teneral and the non-teneral condition ; since the sample consists of flies which have reached the end of a hunger cycle (*i.e.* probing flies), this clearly implies that the post-teneral development is not usually completed in a single hunger cycle. For males the tenerals make up about 22 per cent. of the sample with 16 per cent. in an intermediary condition, suggesting that two hunger cycles are necessary to complete the muscular development. For females the corresponding values are 19 and 32 per cent., which indicates that three hunger cycles may be required in this sex. This difference is in close accord with the fact that the weight increment in males is only two-thirds that in females. Observations on males maintained in the laboratory have shown that under these conditions the increase in weight may be much slower, amounting to no more than 0·5 mg. during the first hunger cycle.

Attention may be drawn to an apparent discrepancy associated with the samples collected in the field : the equality, namely, of the proportion of tenerals in the two sexes (with $N♂ = 64$ and $N♀ = 60$, *chi-square* $= 0{\cdot}08$, $P = 0{\cdot}8 - 0{\cdot}7$) and the close approximation of the sex ratio to unity. For it is generally accepted that females live twice as long as males (Buxton, 1955), but in that case the teneral stage should occupy a correspondingly smaller proportion of the female life span, giving a lower teneral percentage ; and under the conditions of the present sampling method, twice as many females should be caught. Both discrepancies could be accounted for on the assumption that the female hunger cycle is twice as long as that of the male ; but pending independent evidence of such a difference this assumption must be suspect in view of the possibility that sampling errors, so prevalent in this field of research, may be involved.

Discussion

One of the most characteristic differences between teneral and non-teneral flies—the resilience of the thorax—has been shown to be associated with a gradual process of muscular development extending over several hunger cycles. Two of the criteria by which the categories are distinguished, namely the presence or absence of blood in the gut and the firmness of the thorax, are thus seen to be partially independent during early life. That this discrepancy has not been more widely appreciated is a reflection of the fact that flies are at this time scantily represented in normal samples because of their inactivity (that is, their failure to be attracted to a catching party (*see* Jackson, 1948)).

Since the distinction between teneral and non-teneral tsetse flies has proved a useful one in field and laboratory studies, it would be desirable to retain it ; but the ambiguity inherent in the use of two criteria, one of which is all-or-none (unfed/fed, whether partially or fully) while the other is quantitative and extends over a period of many days, should be avoided by defining tenerals simply as *unfed* flies. Flies which have had a single blood meal, and are in process of deteneralisation in respect of muscular development, might be distinguished by the term " immature " from flies which have completed their post-teneral development. And the terms " young " and " old " could be reserved for such mature flies, in accordance with the degree of wing fray and other characteristics of age.

The occurrence of a phase of post-teneral development, dependent on the ability of newly emerged flies to find food for themselves, would seem to be of some significance in relation to reproductive resources, in so far as fewer energy reserves would need to be provided at the beginning of pupal development. The saving implicit in the post-teneral weight increment of 3 mg. RDW characteristic of females would correspond to 9 mg. fresh weight in the newly deposited larva (75 per cent. water content (*see* Bursell, 1958*a*)), even assuming 100 per cent. efficiency in the conversion of food reserves to flight muscle.

But it is tempting to see in the phenomenon of post-teneral development a more particular adaptation to the mode of reproduction of the genus (adenotrophic viviparity, Imms (1957)). It is reasonable to imagine that there would be a balance between development of flight musculature and the load which is destined to be carried. In the case of tsetse females the maximum load carried during the active phase of the hunger cycle will exceed that carried by males by an amount equal to the weight of the fully developed third instar larva. For *G. swynnertoni* this is between 25 and 30 mg. (Bursell, 1958*a*), which constitutes a substantial proportion of the weight of the insect itself. Clearly, if the corresponding difference in wing musculature were manifested early in development by the provision of a corresponding quantity of developmental reserves, then the extra load of females would vary from one pregnancy to the next, depending on the sex of the offspring; and the flight musculature would have to be adjusted to the heavier (female) sex.[2] But by postponing the manifestation of this sex-difference till an extra-uterine developmental stage, the pregnancy load factor is, as it were, reduced to its lowest common denominator with a corresponding gain in reproductive economy.

ACKNOWLEDGMENTS

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[2] In fact the female puparium *is* slightly heavier than the male, but the difference is of a different order of magnitude (less than 0·9 mg. fresh weight in the newly emerged teneral *G. morsitans* (*see* Jack, 1939, Table IV).

EGG DEVELOPMENT OF *HUMBE TENUICORNIS* SCHAUM (ORTHOPTERA : ACRIDIDAE) IN RELATION TO AVAILABILITY OF WATER

By Philip Hunter-Jones and Janetta G. Lambert
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Introduction

The grasshopper *Humbe tenuicornis* Schaum is common throughout tropical Africa, and is reported to have one generation a year in the Sudan (Joyce, 1952) and two in Nigeria (Golding, 1948).

During laboratory studies on its life cycle, some unusual features were noticed in the course of egg development. In particular, eggs showed no evidence of delayed development under moist conditions, but were considerably retarded in drier conditions, although viability was not affected. This ability to withstand relatively dry conditions during incubation forms the subject of the present paper.

Materials and Methods

The original stock of *H. tenuicornis* was sent as eggs from Achimota, Ghana, by Dr. R. F. Chapman in 1958. Since then the stock has been maintained at the Anti-Locust Research Centre under the conditions described by Hunter-Jones (*in press*) for locusts.

Throughout the experiments, only egg pods from parents kept in crowds were used. The eggs were incubated in a constant-temperature room maintained at 30–30·5° C. and 35–45 per cent. relative humidity. Experimental egg pods, or separated eggs, were kept in glass tubes 2·5 cm. in diameter and 7·5 cm. in height. Eggs kept in " dry " conditions were placed in otherwise empty tubes and left uncorked ; those in " moist " conditions were placed on filter paper in the tubes, the paper resting on cotton wool moistened with distilled water, the tubes being lightly corked. The filter paper prevented the eggs from becoming waterlogged. The eggs were weighed in batches after allowing a period of about one minute for surface moisture on the eggs to evaporate. The main stock of *Humbe* egg pods were incubated in moist sand, containing 15 ml. of water to 100 ml. of dry sand.

Description of the Egg Pod

The complete freshly laid egg pod is roughly cylindrical in shape, measuring 25–35 mm. in length and 5–8 mm. in diameter. The eggs, averaging about 40 per pod, are laid in the lower half of the cylinder in a regular order of parallel rows at an angle of 45° to the long axis of the pod. The micropylar end of the eggs is directed to the base of the pod. The eggs are stuck together with a frothy secretion produced by the accessory glands of the female, and more froth forms a coating about one millimetre thick round the whole egg mass, obscuring the shape of individual eggs. The froth covering also extends to the surface of the soil and this " plug " forms the upper half of the egg pod through which the newly hatched nymphs make their way to the surface. Sand or soil particles stick firmly to the froth and so form a more or less rigid pod. When the egg pod is laid in moist sand the froth retains its soft spongy texture, and can easily be separated from the eggs. When laid in dry sand, however, the froth becomes hard and considerable effort is required to detach it from the eggs. In fact, an egg pod from moist sand has a generally soft and spongy texture, while one from dry sand has a rather smaller diameter and is quite hard ; the former is normally straight or slightly curved, the latter invariably more strongly curved, almost U-shaped.

EGG DEVELOPMENT IN THE PRESENCE OF AVAILABLE MOISTURE

Intact, freshly laid egg pods were incubated over moist cotton wool, as described above, and batches of eggs were separated from the pods at intervals and weighed. In this way it was found that water uptake was negligible for the first four days, but that there was then a period of rapid water absorption until the eleventh day, then a further period of non-absorption, or even slight water loss, until the eggs hatched (fig. 1). The total incubation period averaged 23 days (range 22–26).

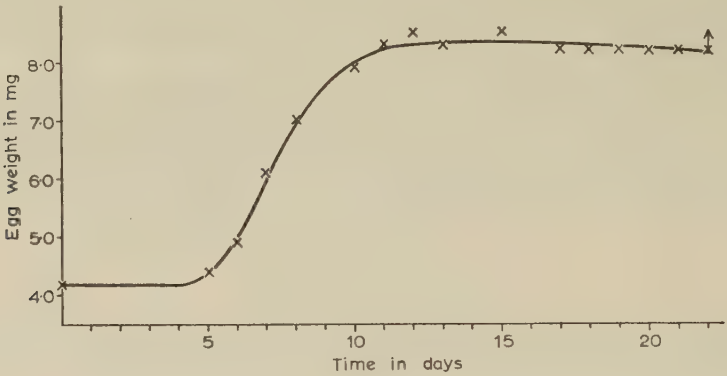

FIG. 1.—Changes in weight of eggs of *Humbe tenuicornis* when incubated under moist conditions.

During the period of water absorption the eggs increased in size, until by the seventh or eighth day the froth covering of the intact pod was split open and the eggs became visible. The total amount of water absorbed amounted to about 95–120 per cent. of the original weight of the egg. The incubation period of the egg pods of the non-experimental main stock, incubated in moist sand, also averaged 23 days.

In other experiments, the eggs were dissected out of the pods within 24 hours of being laid and were incubated as above, but they invariably burst. Similarly, separated eggs that had been laid one, two or three days previously also burst within about 48 hours of being placed on moist cotton wool. Eggs four or more days old, however, absorbed water, developed and hatched in the same time as those left in the intact pods. This suggests that the intact egg pod exerts a protective effect on the eggs, presumably because of the enveloping froth coating, and that there is some change in the egg membranes on the fourth day, by which water uptake is regulated.

Under the above conditions, there was no evidence of obligatory egg diapause. Out of 104 egg pods incubated in one series of experiments, 97 pods hatched well ; the remaining seven pods were unhealthy and completely non-viable.

EFFECT OF DESICCATION

Humbe eggs were kept for part of their incubation period on moist cotton wool in the way described earlier, and were then transferred to open glass tubes at a temperature of 30–30·5° C. and a relative humidity of 35–45 per cent. at daily intervals. Eggs that had been kept in moist conditions for one, two and three days lost weight rapidly after being transferred to conditions of severe desiccation, until after 3–5 days their weight became stable at the dry weight of the egg—about 45–50 per cent. of the total weight of the freshly laid egg. Eggs of rather greater age, that had been incubating in moist conditions for four, five and six days, lost weight at a very much slower rate when placed in dry conditions and the dry weight was not reached for several months. Eggs laid seven or more days previously, however, lost weight rapidly when placed in dry conditions and dry weight was reached in 5–10 days. Three examples are shown in figure 2. Eggs that had been incubated for three days in moist conditions and then transferred to dry conditions (*BB*) lost 46 per cent. of their weight in two days and reached dry weight in five days. Similarly, eggs incubated for 13 days in moist sand before transfer (*AA*) lost 52 per cent. of their weight in three days, and dry weight was reached in 10 days after this transfer. Those of intermediate age, incubated for five days in moist sand before being placed in dry conditions (*BC*), lost only 16 per cent. of their weight in the first five days and after 20 days had lost only 29 per cent. Thus, whereas the eggs were susceptible to desiccation for most of the incubation time, in the short period four to six days after oviposition, they were considerably more resistant. From these three examples and the other records based on the daily removals, it is concluded that some change in the egg membrane occurs in the fourth day that affects the rate of entry and loss of water.

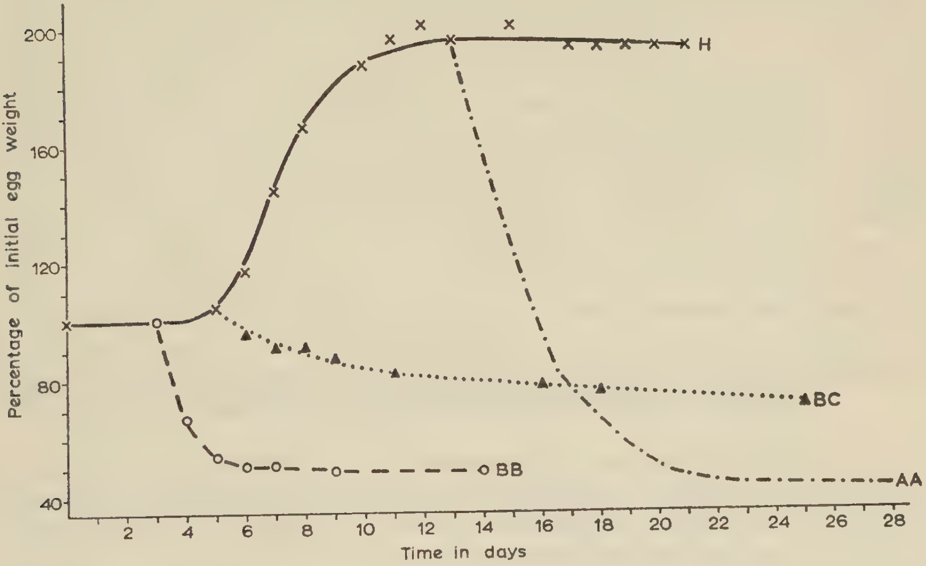

Fig. 2.—Effect of moist and dry conditions on weight of developing *Humbe tenuicornis* eggs. (Eggs kept in moist conditions throughout the incubation period (*H*), eggs kept moist for three days before being transferred to dry conditions (*BB*), eggs kept moist for five days before being kept dry (*BC*) and eggs kept moist for 13 days and then kept in dry conditions (*AA*).)

Effect of Desiccation Followed by Hydration

It has been shown that the eggs hatched in about 23 days when free water was available, but that under dry conditions they lost weight, the rate of loss depending on the age of the egg. Further experiments were undertaken to find out whether this weight loss was reversible, and whether the eggs remained viable. Eggs were again allowed to develop normally on moist cotton wool for different periods before being transferred to dry conditions, and were finally replaced on the moist cotton wool. In this way it was found that the water loss from eggs which had been kept moist for the first 0–3 days before being placed in dry conditions, was not reversible. When replaced on moist cotton wool most of the eggs died, although a small proportion absorbed water and burst. Similarly, eggs kept for seven or more days in moist conditions before desiccation died and no further development took place when they were returned to moist conditions.

In contrast, eggs that had been four to six days in moist conditions, and had reached the stage resistant to desiccation, lost little water during the period in dry conditions, and were able to absorb moisture and continue development when water was again made available. For example, in one experiment eggs were kept for five days on moist cotton wool, then transferred to dry conditions for ten days, and finally returned to moist cotton wool; they re-absorbed water and hatched 14 days after being remoistened (fig. 3). As the normal incubation period was 23 days, and the eggs described above had been kept in moist conditions for only five days before desiccation, it follows that some development probably occurred during the dry conditions. In other experiments, the length of the period of desiccation was extended to five months; these eggs also hatched 14 or 15 days after being placed again in contact with free water. This extension of the incubation period as a result of unfavourable conditions is distinct from a true diapause, where development is arrested spontaneously. Consequently, the period of little or no development will be referred to hereafter as " quiescence ".

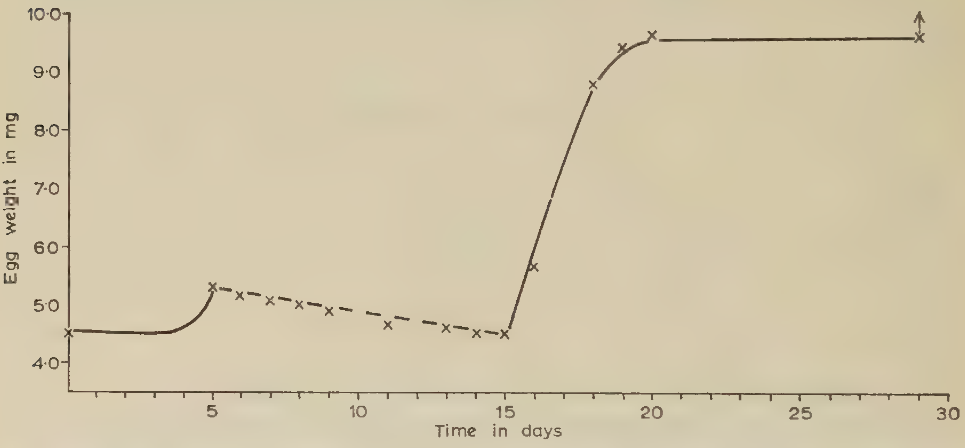

Fig. 3.—Eggs of *Humbe tenuicornis* kept for five days in moist conditions, followed by ten days in dry conditions, and then a further period in moist conditions.

Egg Development in Relation to Choice of Oviposition Sites

A number of sexually mature *Humbe* adults in a cage of about 60 litres capacity were provided with six tubes full of sand in which to lay their eggs. Each tube measured 4 cm. in diameter and 10 cm. in height. Three of the tubes were filled with moist sand (15 ml. of water to 100 ml. of dry sand), while the other three contained moist sand in the bottom half of the tube, and dry sand in the top half. The tubes were changed daily whether eggs had been laid or not, and the positions occupied by the two groups also alternated daily. After three weeks, the grasshoppers had laid 32 egg pods in the moist sand and 28 in the dry sand. As *Humbe* egg pods are usually less than 5 cm. in length (p. 75), it was assumed that the tip of the abdomen did not reach the moist sand, although some blurring of the moist and dry sand interface may have occurred due to capillarity.

The undisturbed egg pods were then incubated at 30–30·5°C., and after about 23 days those laid in moist sand hatched and none became quiescent. Eggs laid in the dry sand, however, did not hatch and all became quiescent. When water was added several weeks later, the quiescent eggs resumed development and subsequently hatched. Thus, the range of tolerance with regard to moisture content of the oviposition sites is wide in this grasshopper species and the type of egg development can be adjusted accordingly. Eggs laid in moist conditions hatch within a few weeks while those laid in dry conditions do not develop until they are moistened by rainfall.

DISCUSSION

This work implies that *Humbe* eggs survive dry conditions in the field by entering a state of quiescence. This state is not obligatory diapause, since it can be terminated at any time by moist conditions. It would be of interest to know how widespread such survival may be among locusts and grasshoppers. A similar quiescent state was found in eggs of the Brown Locust (*Locustana pardalina* (Walk.)) by Matthée (1951) and Remaudière (1954), and Popov (1959) suggested that delayed embryonic development might occur in the African Migratory Locust (*Locusta migratoria migratorioides* (R. and F.)). The incubation period of the Desert Locust (*Schistocerca gregaria* Forsk.) has been extended experimentally by Husain, Ahmad and Mathur (1941) by use of moisture-deficient soils, and by Shulov (1952) in the absence of contact moisture. This capacity for prolonging the egg period in species that can develop quickly could account for the appearance of certain Acridids after rainfall in areas where there has been no recent oviposition.

This quiescent state is necessarily linked with the water-proofing of the eggs. Newly laid eggs appear to be unable to control water intake or loss, and this suggests that the primary wax layer described by Slifer (1948) in *Melanoplus* is not present in *Humbe*. Instead, the froth covering of the egg pod apparently controls the water supply of newly laid eggs. After the fourth day of incubation, however, *Humbe* eggs can themselves effectively control water passage ; this water control is probably associated with the secretion of the so-called secondary wax layer between the yellow and white cuticles described by Matthée (1951) in *Locustana*, and by the formation of the hydropyle, which is completed in three days in *Locusta* (Jones, 1956). Then when the egg is seven or more days old, it again becomes vulnerable to desiccation. By this time, considerable water has been absorbed and the membranes are no longer waterproof, possibly owing to increasing tension or even rupture.

SUMMARY

Eggs of *Humbe tenuicornis* Schaum were incubated on moist cotton wool or in moist sand at 30° C. and hatched after about 23 days. Under these conditions, with water readily available, 93 per cent. of the pods hatched and there was no egg diapause. There was some evidence that the froth covering round the pod exerted a protective influence on the eggs for the first few days of incubation, by preventing too much water reaching them. Other eggs were kept for part of the incubation time in moist conditions and then transferred to dry conditions where water was not available, and kept at a relative humidity of 35–45 per cent. The subsequent rate of water loss was rapid for eggs that had been kept for 0–3 and 7–20 days in moist conditions before transfer, and these eggs reached their dry weight in a few days. Eggs 4–6 days old, however, lost water at a very much slower rate and their dry weight was not reached for several months.

After eggs had been in dry conditions for some time, they were returned to moist conditions. Eggs that had reached their dry weight were no longer viable. Those that were 4–6 days old when subjected to dryness, however, absorbed water when returned to moist conditions and developed normally after as long as five months in dry conditions.

The implications of this extended incubation period are discussed in relation to the survival of eggs in dry conditions in the field.

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A STUDY ON THE POST-EMBRYONIC DEVELOPMENT OF *MACHILOIDES DELANYI* WYGODZINSKY (THYSANURA : MEINERTELLIDAE)

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Introduction

As far as it is known, the post-embryonic development of members of the order Thysanura involves gradual changes in the external characters extending over a comparatively large number of instars (Lindsay, 1940 ; Delany, 1959). Furthermore, it is of note that the taxonomic separation of species is frequently based on relatively minor characters which may possibly not appear until comparatively late in development. In order to establish the changes taking place in one species, as well as the magnitude of the changes, the present paper has been written.

In a recent revision of the order, Remington (1954) included in the suborder Microcoryphia the superfamily Machiloidea and two families of living insects, the Machilidae and the Meinertellidae. Accounts have appeared of the post-embryonic development of members of the former family (Verhoeff, 1910 ; Delany, 1959) but information has not previously been obtained on the Meinertellids. The following account deals with a member of this family, *Machiloides delanyi* Wygodzinsky, and outlines the post-embryonic development in rather more detail than do the earlier descriptions of the Machilids.

The author is indebted to Dr. E. McC. Callan of the University of Grahamstown for supplying the material.

Materials and Methods

Twenty-two specimens of *M. delanyi* were collected between April and December, 1957, in the vicinity of Grahamstown, South Africa. Of these, the 11 largest individuals were selected, and nine of them were sent to Dr. P. Wygodzinsky for identification and description. The remaining two, a male and female (both adult), with five immature males and one immature female selected from the other eleven smaller individuals, whose body-lengths ranged from 4·5 to 8·0 mm., have been examined in detail. Their lengths were 13, 13·5, 4·5, 5·5, 6, 8, 8, and 6·5 mm., and they had 53 (approximately), 55 (approximately), 18, 25, 31, 36, 41, and 32 rings of scales, respectively, on the lateral cercus.

Delany (1959) found the number of rings of scales (subsequently referred to as annuli) on the lateral caudal cercus to be a useful indication of stage of development of *Petrobius brevistylis* Carpenter. They are a more reliable guide than body-length, as segments may telescope to varying extents at the time of fixation. From the material available it has not been possible to identify instars. As a result, the subsequent account refers to immature insects by the number of annuli each possesses.

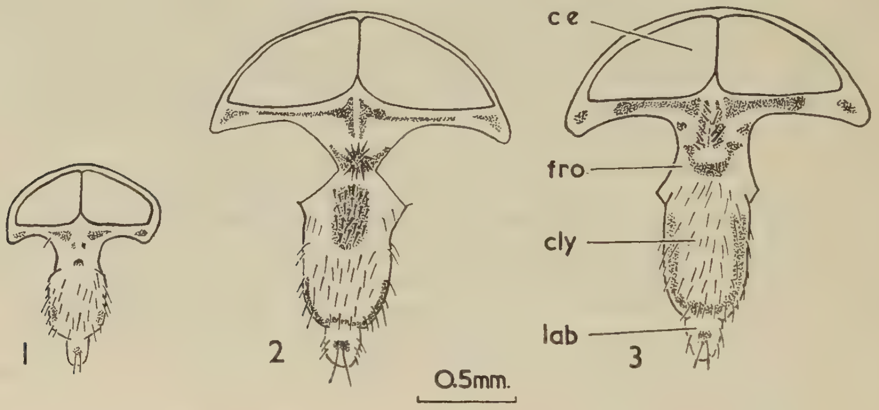
Permanent preparations, mounted in Canada balsam, were made of the head, mouthparts, legs, ventral abdominal segments, genitalia and caudal processes of each of the above insects. A single preparation was stained with acid fuchsin. All illustrations were made with the aid of a camera lucida. The smallest individual was identified as a male during dissection but its genitalia were subsequently lost.

PROC. R. ENT. SOC. LOND. (A) 36. PTS. 4–6. JUNE, 1960.

Descriptions of Development

Head

The 25-annulus male (fig. 1) and the 32-annulus female are without stout setae on the anterior part of the head. In the adult male (fig. 2) a group of stout setae appears on the frons and another on the clypeus, whilst the adult female (fig. 3) possesses a single group of setae situated on the frons slightly dorsal to the comparable group in the male. In the male, these setae first appear at the 36-annulus stage, when two were observed on the clypeus and five on the frons. Pigmentation increases as growth proceeds. Some of the dark areas below the compound eyes probably represent ocelli, although these structures were not distinct.



Figs. 1–3.—Anterior aspect of head, excluding the antennae, of *Machiloides delanyi* Wygodz.: (1) 25-annulus male; (2) adult male; (3) adult female. (*ce*, compound eye; *cly*, clypeus; *fro*, frons; *lab*, labrum.)

Mouthparts

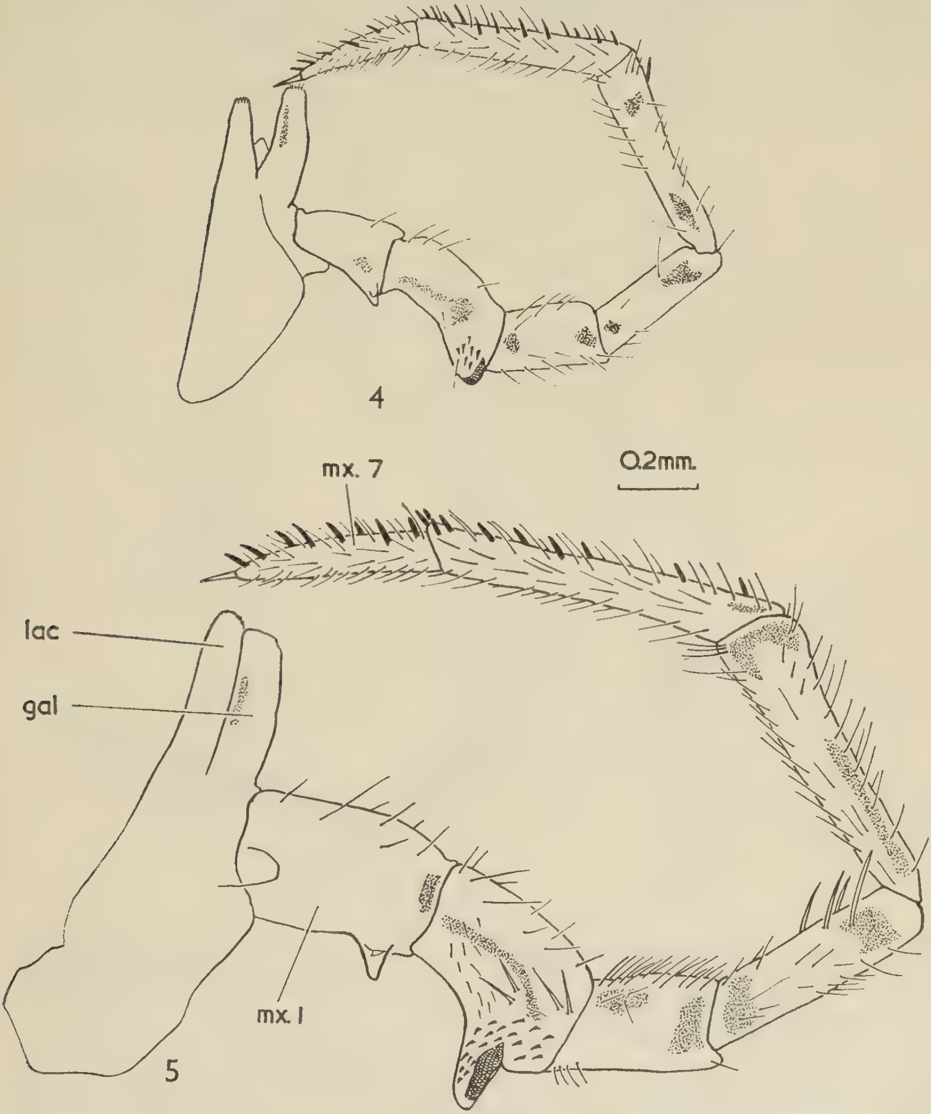
The structure of the mandible is similar to that generally seen in the Microcoryphia and shows a steady increase in size as the animal grows. Pigmentation occurs mainly on the outer margin of the proximal portion.

The maxilla of the adult male (fig. 5) is characterized by the presence on the hinder margin of its second segment of a crenulated surface surrounded by a group of 20 short, stout setae. Internal to these, and also on the inner margin of the fourth segment, are two small groups of long straight setae (fig. 5). The appearance of these structures follows a definite sequence. At the 18- and 25-annulus stages they are absent; the crenulated surface first appears at the 31-annulus stage and the setae around it at the 36 (fig. 4). The larger spine-like setae do not appear until later than the 41-annulus stage. There is a general increase in the number of setae on the maxilla and the blunt setae of the seventh segment are not present at the 18-annulus stage. The lacinia is comparatively small during the early development. The second segment in the adult female is devoid of the structures present in the male and at the 32-annulus stage the distribution of setae is similar to that in the 25- and 31-annulus stages of the male. Pigmentation is more widespread in the female.

The number of sensory setae at the tip of the terminal segment of the labial palp gradually increases, 6, 7, 8, 9 and 12 setae being counted at the 18-, 25-, 31-, 41-annulus and adult stages, respectively, in the male; the female with 31 annuli had 7 and the adult female, 12.

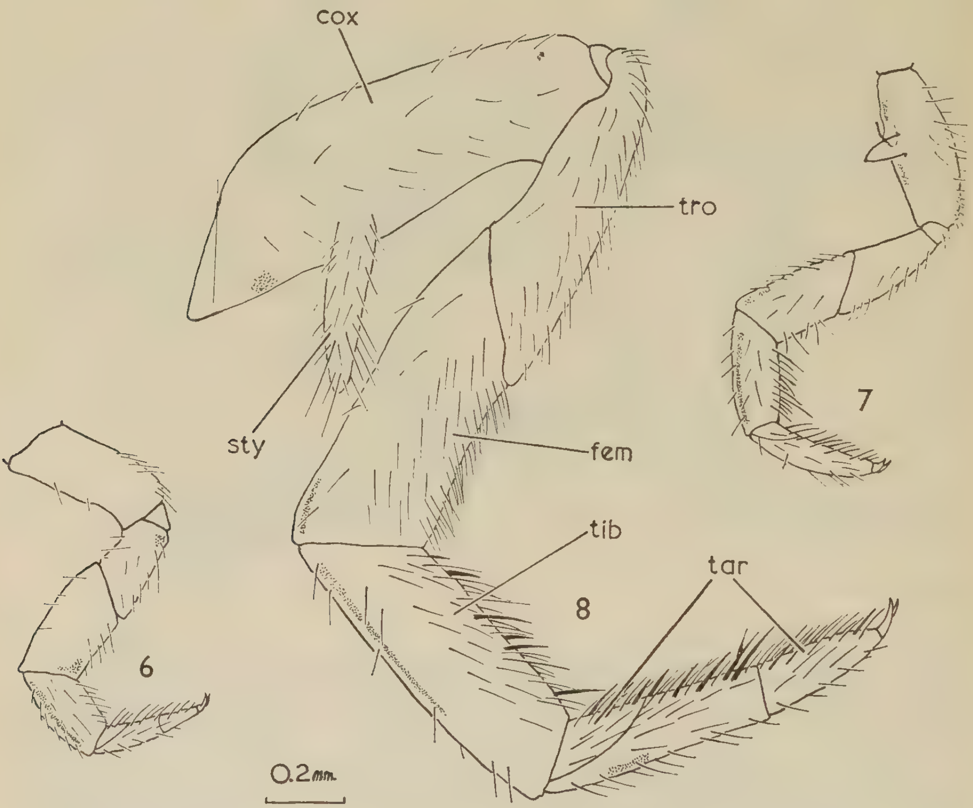
Legs

In the 18- (fig. 6) and 25-annulus stages the setae of the prothoracic tarsi and tibiae are uniform whereas later, larger setae appear and become progressively more numerous. This developmental pattern is repeated in the meso- and meta-thoracic limbs, except that in the 36-annulus male the latter have no larger setae. At the 18-annulus stage the subdivision of the tarsus into second and third segments is indistinct in the prothoracic leg and absent from the meso- and meta-thoracic legs (fig. 7). Lindsay (1940) records *Ctenolepisma* as having two tarsal segments on each leg in the first instar, three on the metathoracic leg in the second and three on all legs in the third.



FIGS. 4 and 5.—Maxilla of *Machiloides delanyi* Wygodz., male : (4) 36-annulus ; (5) adult. (*gal*, galea ; *lac*, lacinia ; *mx*1, *mx*7, first and seventh segments of maxillary palp.)

The mesothoracic style increases its relative size according to an irregular pattern. At the 18-, 25-, 31-, 36-, 41-annulus and adult stages the ratios of style length to coxa length are 0·21, 0·26, 0·25, 0·48, 0·47 and 0·50 respectively. Initially, the metathoracic style grows more rapidly than the mesothoracic. In the first three stages (fig. 7) the ratios of style length to coxa length are 0·19, 0·33 and 0·45. Thus, at the 31-annulus stage the style is comparatively longer on the metathoracic than on the mesothoracic limb. For the 36-, 41-annulus and adult stages (fig. 8) the ratios are 0·40, 0·45 and 0·43 respectively. Delany (1959) noted that thoracic styles did not appear on *Petrobius* before the 10–16-annulus stage. They were then small protuberances whose ratio of length to coxa length was 0·06. In the 17–22- and 23–29-annulus stages the ratios were 0·21 and 0·31. These figures are comparable with the 18- and 25-annulus stages of *Machiloides* and suggest that the style is a rapidly growing structure. That it is possibly absent from the earliest instars is supported by Tillyard's (1932) record of the absence of styles from newly hatched specimens of *Allomachilis*, another Meinertellid.



Figs. 6–8.—Legs of *Machiloides delanyi* Wygodz., male : (6) prothoracic leg of 18-annulus stage ; (7) metathoracic leg of 18-annulus stage ; (8) metathoracic leg of adult. (*cox*, coxa ; *fem*, femur ; *sty*, style ; *tar*, tarsus ; *tib*, tibia ; *tro*, trochanter.)

In each leg the adult female has more widespread pigmentation of the tibia and tarsi than the male, whilst in the young female pigment is lacking.

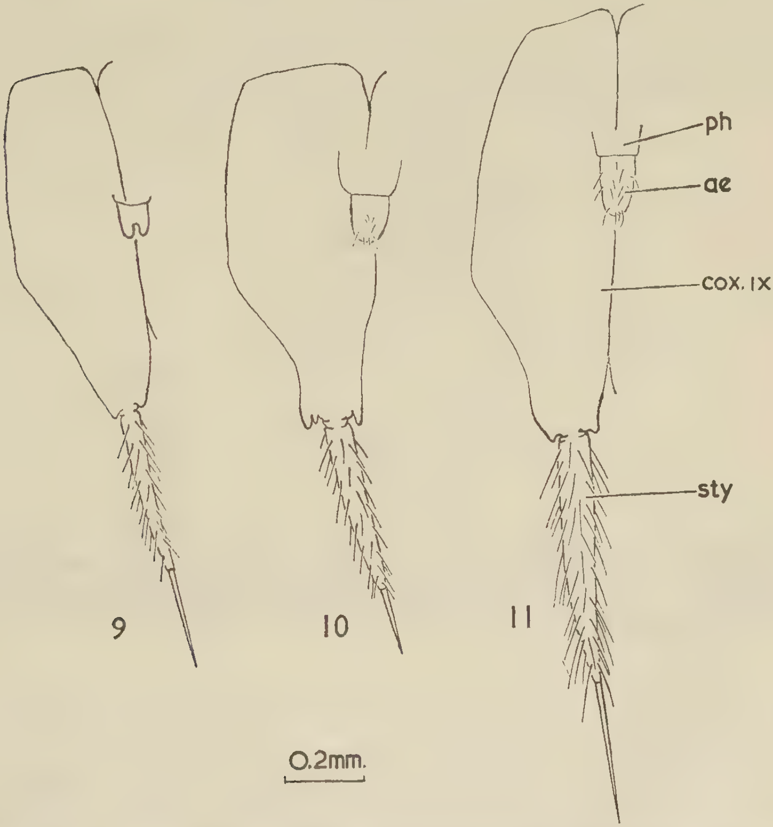
Abdominal segments

In all the insects examined the coxal vesicles were fully formed. The style in the young male is relatively shorter than in the adult (Table I). This feature is

TABLE I.—*Ratios of lengths of abdominal styles (excluding terminal spine) to coxopodites in* Machiloides delanyi *Wygodzinsky*

Number of annuli	Sex	Abdominal segments II–VII	VIII	IX
18	♂	0·44–0·52	0·44	.
36	♂	0·44–0·51	0·51	0·59
41	♂	0·44–0·50	0·61	0·63
Adult	♂	0·50–0·55	0·80	0·76
32	♀	0·42–0·49	0·50	.
Adult	♀	0·41–0·45*	0·57	0·56

* Excluding segment VII, where a pair of posterior lobes on the coxites make the ratio 0·36.



FIGS. 9–11.—Stages in development of male external genitalia of *Machiloides delanyi* Wygodz. as viewed dorsally: (9) 25-annulus; (10) 31-annulus; (11) 36-annulus. (*ae*, aedeagus; *cox. ix*, coxopodite of abdominal segment IX; *ph*, phallobase; *sty*, style.)

particularly noticeable in segments VIII and IX. In the 36-annulus stage, the coxopodite of segment VIII is no longer than those of segments II–VII. It subsequently grows more rapidly and in the adult is slightly longer than in the preceding segments. The style increases its size with greater rapidity. Both coxopodite and style of segment IX are longer, at all stages, than those of segments II–VIII with the style increasing its length more rapidly than the coxopodite.

The ratio of style length to coxopodite length in segments II–VI is similar for both adult and immature females. In the adult, coxopodite VII is lengthened by the presence of a postero-median lobe; coxopodite VIII is slightly longer than, and coxopodite IX twice as long as, coxopodites II–VI.

External genitalia

The aedeagus of the adult is relatively small and arises from the dorso-median margin of the coxopodites of segment IX. The 25-annulus stage was the earliest examined in detail. Here (fig. 9), the aedeagus has a small posterior cleft similar to that seen in the early development of *Petrobius* (Delany, 1959). The subsequent development involves the loss of the cleft, a covering of setae and a slight elongation of the aedeagus (figs. 10 and 11).

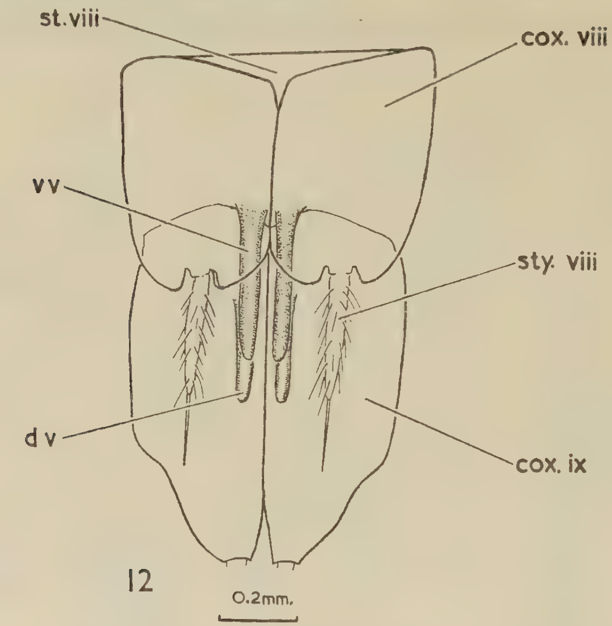


Fig. 12.—Ventral aspect of abdominal segments VIII and IX of 32-annulus female of *Machiloides delanyi* Wygodz. (*cox. viii, cox. ix*, coxopodites of segments VIII and IX; *dv*, dorsal valve of ovipositor; *st. viii*, sternite of segment VIII; *sty. viii*, style of segment VIII; *vv*, ventral valve of ovipositor.)

The valves of the ovipositor of the immature female are without annulations and setae, and the two pairs are of unequal length (fig. 12). *Petrobius* displays similar characters at the 23–29-annulus stage (Delany, 1959). Owing to the incompleteness of the present series it is only possible to compare the single immature stage with the adult. The ovipositor valves of the adult are annulated, covered in setae and extend approximately eleven-twentieths of their length beyond the coxopodites of segment IX.

Discussion

The development of *Machiloides* has been traced from a collection of insects with body-lengths ranging from 4·5 to 8·0 mm. and compared to adults with body-lengths of 13·0 and 13·5 mm. The 8 mm. individual differed from the smaller (4·5 mm.) individual in external appearance more than it did from the adult, so that the first change apparently involves both growth and differentiation, and the second, only growth. No insects smaller than 4·5 mm. were collected and as the first instar of other members of the suborder is approximately 2·5 mm. long, it appears that the changes involved in the first two millimetres of growth await description.

As far as they are known, the changes witnessed in the development of *Petrobius* (Delany, 1959) appear similar to those in *Machiloides*, although comparison is hampered by the dissimilarity of certain structures in the adult, *e.g.* male genitalia, number of coxal vesicles. The similarities include the gradual increase in the number of sensory setae on the labial palp, the cleft aedeagus and the non-annulated ovipositor valves.

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BOOK NOTICES

Bionomics, systematics, and phylogeny of Lytta, *a genus of blister beetles* (*Coleoptera, Meloidea*). By R. B. Selander. 8vo. University of Illinois Press, 1960. [Illinois Biological Monographs. No: 28.] Pp. vi + 295, text illust. Paper bound $4.50, cloth bound $5.50.

This work is an attempt to define the genus *Lytta* on a world basis. For the main, it is devoted to the revision of the species of the North American continent, with consideration of the Old World fauna confined mainly to evolutionary lines. The classification proposed is a phylogenetic one. A section on bionomics, which is a summary of available information concerning the development, habits and ecological relationships of the species of the genus, includes sections on economic importance, enemies, activities of adults and development of immature stages. The major part of the work is devoted to systematics and phylogeny. This contains sections on the limits of the genus, classification, distribution and the various subgenera. There is also an artificial key to the North American species, keys to the subgenera, a long list of references, an index, and numerous text figures.

Bulletin of the California Insect Survey. Vol. 6. No. 4. The Siricid wood wasps of California (Hymenoptera: Symphyta). By W. W. MIDDLEKAUFF. Pp. 59–77, text illust. 4to. Berkeley and Los Angeles, University of California Press, 1960. Price $0.50.

Vol. 6. No. 5. The soldier flies or Stratiomyidae of California. By M. T. JAMES. Pp. 79–122, text illust. 4to. Berkeley and Los Angeles, University of California Press, 1960. Price $1.00.

The above works are among the most recent additions to the California Insect Survey Bulletins. In the first work the author states that, previously, North American species of Siricid wood wasps have been neglected and little was known about them. An account of their biology is given and there are notes on four genera and thirteen species, as well as keys to subfamilies, genera and species. There are 20 figures and a list of references.

The second work is intended to fulfill part of the need for a comprehensive survey of the Stratiomyidae of the Pacific coast, although the author has omitted two groups which he hopes to include in a supplement. It includes a key to subfamilies and genera, keys to species and brief notes on their biology, maps showing distribution, a list of 11 references, and 56 figures illustrating abdominal patterns, head forms, wings and genitalia.

The beetles of the United States (*A manual for identification*). By R. H. ARNETT. Section 1. Fasc. 1–9, pp. xi + 210. Washington: Catholic University of America Press, 1960. $3.50 (Binder $3.95 extra).

This is the first of approximately eight sections which the publishers estimate will take two years to complete. The work is intended to bring up to date in a completely revised form Bradley's *A manual of the beetles of America, north of Mexico*, and to provide a tool for the identification of adult beetles of the United States in family and genus with the aid of illustrations, keys, references to sources of keys, and descriptions of the species of the area.

The introduction contains advice on the use of the various fascicles of which the work is composed and each of which deals with a single family, a definition of the area covered, and a description of the external anatomy of adult beetles. There is also a scheme of clasification for Coleoptera, a key to beetle families of the world, a bibliography of general works and an index. The remainder of section 1 contains nine fascicles on Cupedidae, Rhysodidae, Cicindelidae, Carabidae, Amphizoidae, Haliplidae, Dytiscidae, Noteridae, and Gyrinidae.

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Papers offered for publication in the *Transactions* are considered by the Publication Committee of the Society which meets usually in the months of May and November. In order that papers may be considered at these meetings it is necessary for the manuscript and drawings for illustrations to be in the hands of the Registrar as early as possible. Papers received *after* 1st April and 1st October cannot be considered at the meeting immediately following.

The Society is prepared to undertake the provision of a reasonable number of figures, in line or half-tone. Colour work is accepted only by special arrangement.

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TO BE HELD IN THE SOCIETY'S ROOMS
41, Queen's Gate, S.W.7

1961

Wednesday, July 5
Thursday/Friday (Symposium) Sept. 21–22
Wednesday, October 4

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